UNIVERSITÉ DU QUÉBEC EN ABITIBI-TÉMISCAMINGUE

DÉTERMINATION DE L'IMPORTANCE DES CAVITÉS EN PÉRIODE HIVERNALE ET UTILISATION DE L'HABITAT PAR LE GRAND POLATOUCHE (GLAUCOMYS SABRINUS) EN FORÊT BORÉALE MIXTE DE L'EST DU CANADA.

MÉMOIRE

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AVANT-PROPOS

Conformément aux exigences du programme de maîtrise en biologie, ce mémoire comprend deux articles rédigés en langue anglaise portant sur l'importance des cavités en période hivernale et l'utilisation de l'habitat par le Grand Polatouche en forêt boréale mixte, ainsi qu'une introduction et une conclusion générales. Le premier article porte plus spécifiquement sur l'utilisation de l'habitat à l'échelle du paysage et le second article quant à lui porte sur l'importance des cavités en période froide. Les deux articles seront soumis au périodique scientifique *Canadian Journal of Zoology*. J'ai procédé à toutes les étapes de collecte, de traitement et de l'analyse des données pour ces deux articles en plus d'en être la première auteure. Louis Imbeau, Pierre Drapeau et Marc Mazerolle en sont les co-auteurs.

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RÉSUMÉ

Depuis l'adoption en 2001 d'une nouvelle loi sur les forêts souscrivant aux principes de développement durable, le maintien de la biodiversité est devenu un enjeu de poids pour l'aménagement forestier au Québec. Pour atteindre cet objectif, certains auteurs suggèrent de conserver les cavités qui constituent une ressource faunique importante autour de laquelle interagissent les pics, certains oiseaux forestiers et d'autres petits mammifères tels que le Grand Polatouche (*Glaucomys sabrinus*). Ce dernier est un rongeur arboricole nocturne qui utilise les cavités comme refuge diurne et site de mise bas, et pour lequel l'utilisation de l'habitat est peu connue en forêt boréale de l'est du Canada. Puisque les cavités sont souvent peu disponibles en forêt boréale et qu'elles pourraient offrir une isolation thermique supérieure à celle d'autres types de nids, les cavités ont le potentiel de limiter la présence du Grand Polatouche dans un climat rigoureux. L'objectif de cette étude était de déterminer si les cavités affectent l'utilisation de l'habitat par le Grand Polatouche et de décrire les caractéristiques des nids utilisés en période hivernale. En forêt boréale, puisque la majorité des cavités sont excavées dans le Peuplier faux-tremble (*Populus tremuloides*), nos hypothèses étaient que le Grand Polatouche utiliserait les forêts matures de feuillus et qu'il éviterait les milieux ouverts qui nuisent à sa dispersion. Aussi, le Grand Polatouche occuperait les sites avec une plus grande disponibilité de cavités et il préfèrerait les cavités comme refuge en période froide. Nous avons déterminé les facteurs d'habitat qui influençaient l'occupation de site et les facteurs climatiques qui affectaient la probabilité de détection de l'espèce à différentes échelles spatiales. D'abord, nous avons visité 149 paires de nichoirs à l'hiver 2008 et utilisé un SIG pour extraire des variables de composition du paysage à partir des cartes écoforestières. Ensuite, nous avons piégé 59 sites feuillus représentant un gradient de disponibilité de cavités à l'automne 2008 et échantillonné ces peuplements pour quantifier les variables d'habitat susceptibles d'influencer l'occupation de site par le Grand Polatouche. Finalement, 46 individus parmi les 85 individus capturés ont été suivis par télémétrie entre septembre 2008 et juin 2009 afin d'identifier leurs refuges diurnes, et de tester l'effet de la température sur leur sélection. Les résultats supportent partiellement nos hypothèses. À l'échelle du paysage, le Grand Polatouche évite les forêts de conifères et ne semble pas être influencé par la proportion de forêt mature ou de milieux ouverts. De plus, à l'échelle du peuplement, il a été détecté dans 58% des sites échantillonnés dominés par le Peuplier faux-tremble. Par contre, la disponibilité de cavités n'influence pas l'occupation de sites par le Grand Polatouche. À l'échelle du nid, les localisations télémétriques montrent qu'en période hivernale les femelles utilisent principalement les nids au sol (44%) alors que les mâles semblent sélectionner surtout les nids externes (57%). Lorsque la température diminue, les femelles comme les mâles évitent les cavités, leur préférant respectivement les nids au sol et les nids externes. Les résultats confirment que les forêts de feuillus sont importantes pour le Grand Polatouche en forêt boréale de l'est du Canada. De plus, bien que les cavités soient utilisées par le Grand Polatouche, celles-ci ne semblent pas représenter un facteur limitant l'espèce en période froide.

Mots clés : *Glaucomys sabrinus*, nid, climat froid, télémétrie et occupation de site.

INTRODUCTION GÉNÉRALE

Problématique

Au Québec, la conservation de la diversité biologique est devenue une préoccupation importante en aménagement forestier durable avec les modifications apportées aux différents régimes de loi. En 2001 et 2010, l'Assemblée nationale du Québec adoptait des modifications à la Loi sur les forêts (Loi modifiant la Loi sur les forêts et d'autres dispositions législatives, projet de loi #136 et Loi sur l'aménagement durable du territoire forestier, projet de loi #57) qui incluent la conservation de la diversité biologique à titre d'un des six critères de développement durable. Subséquemment, le Ministère des Ressources naturelles et de la Faune du Québec a modifié le Règlement sur les normes d'interventions dans les forêts du domaine de l'État (RNI) pour y inclure des clauses obligeant l'industrie forestière à considérer le maintien de la biodiversité dans leurs plans d'aménagement forestier. Cependant, la mise en application de plans de conservation de la biodiversité nécessite des connaissances approfondies sur les espèces ainsi que sur les processus régissant la dynamique naturelle des écosystèmes forestiers.

Sur le plan théorique, il a récemment été suggéré que les stratégies de conservation soient structurées autour des processus écologiques clés ('keystone processes') qui regroupent plusieurs espèces autour d'une ressource essentielle (Bednarz et al. 2004). En forêt boréale de l'est du Canada, les chicots et les gros arbres ayant des cavités en sont un exemple puisqu'ils fournissent des substrats d'alimentation, des sites de repos et des cavités de nidification à plus d'une cinquantaine d'espèces d'oiseaux et de mammifères (Darveau et Desrochers 2001). Les cavités ont donc été reconnues comme la ressource critique au cœur d'un réseau complexe d'utilisateurs, appelé 'nest webs' (Martin et Eadie 1999; Aitken et al. 2002), qui relie les excavateurs primaires créant la ressource, à des excavateurs faibles et utilisateurs secondaires qui y nichent. La rétention des arbres à cavités pourrait ainsi permettre le maintien d'un ensemble d'espèces associées à ce type de structure.

Le Grand Polatouche

Le Grand Polatouche (*Glaucomys sabrinus*) est un rongeur arboricole dont la distribution couvre le Canada et le nord des États-Unis, avec quelques populations isolées dans les montagnes côtières américaines. Il est associé aux forêts matures et il niche dans des cavités ou des nids construits dans la canopée. Il est incapable de construire les cavités qu'il utilise et dépend des excavateurs primaires ainsi que des processus naturels pour leur création. Il utilise les cavités comme refuge, site de repos ou site de mise bas et d'élevage des petits. Puisque cette espèce est sensible aux modifications de son habitat (Holloway et Malcolm 2006) et qu'elle est utilisée à titre d'espèce indicatrice d'aménagement durable en Amérique du Nord (McLaren et al. 1998), elle est une espèce de choix pour élucider l'importance des cavités et leur utilisation spécifique. Plusieurs études ont été entreprises sur la côte ouest du Pacifique où il y est considéré comme la proie principale de la chouette tachetée (*Strix occidentalis*), une espèce menacée. Par contre, peu d'études ont porté sur cette espèce dans l'est de son aire de répartition.

Sélection d'habitat

L'habitat optimal du Grand Polatouche se compose de forêts contigües de conifères avec une forte composante d'épinettes (Payne et al. 1989; McDonald 1995; Holloway et Malcolm 2006; Menzel et al. 2006). Par contre, le Grand Polatouche a aussi été associé aux forêts mixtes ou décidues dans certaines régions (Wells-Gosling et Heaney 1984) et ne semble pas préférer l'un ou l'autre dans des conditions expérimentales (Weigl 1978). Certains auteurs ont aussi observé une corrélation positive entre la densité de population du Grand Polatouche et les attributs de forêts matures tels les gros chicots (Carey 1995; Carey et al. 1999; Holloway et Malcolm 2006), les gros arbres (Gerrow 1996; Smith et al. 2004; Holloway 2006; Lehmkuhl et al. 2006), le bois mort au sol (Carey et al. 1999; Smith et al. 2004) et l'abondance de champignons hypogés (Waters et Zabel 1995; Gomez et al. 2005; Lehmkuhl et al. 2006). Malgré cela, il peut aussi se maintenir dans des forêts plus jeunes et n'est pas considéré strictement dépendant des vieilles forêts (Carey 1989). D'ailleurs, certains auteurs ont trouvé que les densités de Grand Polatouche ne changeaient pas entre jeunes et vieux peuplements et que les jeunes forêts ne représentaient pas des habitats suboptimaux (Rosenberg et Anthony 1992; Ransome et Sullivan 2003; Wheatley et al. 2005).

Les populations de Grand Polatouche peuvent se maintenir dans une matrice de zones agricoles (Bayne et Hobson 1998; Bowman et al. 2005) de même que dans les forêts résiduelles (Côté et Ferron 2001). Par contre, le Grand Polatouche évite complètement les coupes totales (Lomolino et Perault 2001). Il a été suggéré que les habitats ouverts de plus de 75 m constituent un obstacle à la dispersion des polatouches puisque le vol plané, le moyen de déplacement principal, n'est plus possible entre les arbres trop distants (Bendel et Gates 1987). La taille des domaines vitaux est variable, mais ils sont en moyenne plus grands chez les mâles (3.7-59.8 ha) que les femelles (3.4-15.3 ha) dans une même région géographique (Smith 2007). Les domaines vitaux sont aussi généralement plus grands dans des paysages fragmentés ou dans des habitats de moindre qualité (Lehmkuhl et al. 2006; Menzel et al. 2006).

Le Grand Polatouche utilise principalement deux types de nids : les cavités (naturelles ou excavées par les pics) et les nids externes de feuilles ou d'herbe (Wells-Gosling et Heaney 1984). Cependant, l'utilisation de nids souterrains a récemment été observée de façon répétée par certains auteurs (Gerrow 1996; Bakker et Hastings 2002; Hackett et Pagels 2003) et ce type de nid pourrait aussi être commun (Hackett et Pagels 2003). Les nids externes sont fréquemment localisés à l'intérieur de structures communément appelées balais de sorcière (Mowrey et Zasada 1984; Gerrow 1996; Cotton et Parker 2000; Bakker et Hastings 2002) et qui sont le résultat du développement excessif de rameaux de conifères infectés par le champignon faux-gui (*Arceuthobium sp.*) ou la rouille de l'épinette (*Chrysomyxa sp.*). Carey et al (1997) rapportent que chaque individu utilise deux types de nids ou plus.

La proportion relative des divers types de nids utilisés varie entre les différentes régions géographiques de même qu'à l'intérieur de celles-ci, et semble être largement influencée par des facteurs qui affectent la disponibilité de sites convenables (Carey et al. 1997). Smith (2007) rapporte des pourcentages d'utilisation de cavités variant de 35 à 84% dans sa synthèse de huit études réalisées à travers l'aire de répartition du Grand Polatouche. Dans une même région, les caractéristiques des arbres à nids (diamètre, âge, taille) varient grandement, mais le Grand Polatouche sélectionne constamment les arbres plus gros, plus hauts et plus âgés dans l'éventail des arbres disponibles (Cotton et Parker 2000; Bakker et Hastings 2002; Menzel et al. 2004; Meyer et al. 2007). L'utilisation des différents types de nids change en

fonction de la saison et du partage des nids par plusieurs individus. Notamment, les femelles reproductives au printemps sélectionnent les cavités comme site de mise bas (Gerrow 1996; Carey et al. 1997; Holloway et Malcolm 2007). De même, les températures plus froides en hiver favorisent l'utilisation des nids souterrains (Gerrow 1996) et de cavités (McDonald 1995; Gerrow 1996; Cotton et Parker 2000). L'agrégation de plusieurs individus dans les nids est fréquemment observée et parfois liée à la baisse des températures (Muul 1968; Gerrow 1996). Les grandes cavités sont ainsi importantes pour l'agrégation et les sites de mise bas (Gerrow 1996; Carey et al. 1997).

Facteurs limitants

Les trois principaux facteurs ayant le potentiel de limiter les populations de Grand Polatouche sont la disponibilité de nids, la disponibilité de nourriture et la prédation (Carey 2002). La disponibilité de nids est le facteur qui a été le plus étudié. Les études récentes ayant expérimenté l'addition de nichoirs artificiels n'ont obtenu aucune augmentation de l'abondance de la population ou du taux de reproduction (Carey 2002; Ransome et Sullivan 2004) et les mêmes résultats ont été obtenus chez le Petit Polatouche (Brady et al. 2000). Malgré tout, certains auteurs considèrent encore que les cavités pourraient être limitantes dans certaines circonstances, notamment lorsqu'il y a une forte compétition intraspécifique (Smith 2007) ou lorsque de grosses cavités sont nécessaires à l'agrégation de plusieurs individus (Maser et al. 1981) comme pour l'élevage des petits (Carey et al. 1997). Les températures froides pourraient aussi forcer le Grand Polatouche vers les cavités puisque ces dernières sont généralement reconnues comme offrant un meilleur isolant thermique que les nids externes (Smith 2007).

La disponibilité de nourriture est la ressource ayant le plus de poids à titre de facteur limitant les populations de Grand Polatouche dans toute son aire de répartition (Ransome et Sullivan 1997, 2004; Smith 2007). Pourtant, le Grand Polatouche a une diète très diversifiée. Il est généralement reconnu comme un mycophage important s'alimentant de champignons hypogés et épigés (Currah et al. 2000; Pyare et al. 2002; Meyer et al. 2005a; Wheatley 2007). Il consomme aussi des noix, graines de conifères, bourgeons, chatons et graines de feuillus, lichens, fruits et insectes (Wells-Gosling et Heaney 1984). Lehmkuhl et al. (2006) ont observé que la densité de population, la survie et le recrutement étaient positivement corrélés

à l'abondance de truffes. De même, la biomasse de lichen et la richesse des espèces de sous-couvert, une mesure de disponibilité de nourriture, montraient une corrélation avec la survie (Lehmkuhl et al. 2006). Les attributs d'habitats auxquels sont associés la présence ou une densité élevée de Grand Polatouche sont aussi corrélés à l'abondance de truffes, tels les débris ligneux au sol (Carey et al. 1999). Plusieurs auteurs ont aussi observé que la localisation des noyaux d'activité ('core area') dans les domaines vitaux coïncide avec la disponibilité de la ressource alimentaire (Gerrow 1996; Meyer et al. 2005b; Holloway 2006). De même, la différence de superficie entre les aires minimales incluant tous les nids ('core nest area') et les domaines vitaux, ces derniers étant jusqu'à 10 fois plus grands, suggère que la nourriture détermine la taille du territoire nécessaire à la survie (Wilson et al. 2008). Par contre, deux études ont examiné l'effet de la nourriture par l'addition expérimentale de celle-ci en Colombie-Britannique et elles ont montré des densités de populations deux fois plus élevées (Ransome et Sullivan 1997) et une survie plus élevée (Ransome et Sullivan 2004) lorsque la nourriture était abondante, mais l'addition de nourriture réduisait considérablement la probabilité de capture et augmentait l'immigration. Ces études ne supportent que partiellement l'hypothèse que la disponibilité de nourriture pourrait être un facteur limitant pour la distribution du Grand Polatouche.

La prédation est le facteur limitant qui a le moins de support empirique (Smith 2007). En Abitibi, les principaux prédateurs aviaires du Grand Polatouche incluent la Chouette rayée (*Strix varia*), le Grand-duc d'Amérique (*Bubo virginianus*), l'Autour des palombes (*Accipiter gentilis*) et la Buse à queue rousse (*Buteo jamaicensis*). Les mammifères incluent la Martre d'Amérique (*Martes americana*), l'Hermine (*Mustela erminea*), le Chat domestique (*Felix catus*), le Loup (*Canis lupus*), le Lynx (*Lynx lynx*) et le Renard roux (*Vulpes vulpes*) (Wells-Gosling et Heaney 1984; Wilson et Carey 1996). Les observations de certains auteurs d'une baisse de densité du Grand Polatouche dans les peuplements où niche la Chouette Tachetée dans l'ouest américain (Carey et al. 1992; Rosenberg et Anthony 1992; Waters et Zabel 1995) représentent une des seules démonstrations d'un effet possible de la pression de prédation sur les populations de Grand Polatouche. Cette suggestion est supportée par l'observation que le Grand Polatouche constitue la proie principale de la Chouette tachetée dans certaines régions de sa distribution (Carey et al. 1992; Hamer et al. 2001; Forsman et al.

2001) et qu'un couple peut en consommer jusqu'à 500 par année dans le Nord-Ouest du Pacifique (Heinrichs 1983). De plus, les densités de certaines populations de prédateurs, telle la Martre d'Amérique, semblent associées à la densité de Grand Polatouche ce qui suggère un lien important de prédation (Fryxell et al. 1999), mais ne certifie pas un effet limitant sur les populations de Grand Polatouches.

Les effets de la perte d'habitat et de la fragmentation du couvert forestier sur le Grand Polatouche n'ont pas été beaucoup étudiés, mais on reconnait qu'ils constituent les causes principales qui menacent le Grand Polatouche dans les Appalaches (Weigl 2007). Par contre, ces effets sont mieux connus chez le Polatouche de Sibérie (*Pteromys volans*) qui a subi une réduction considérable de sa distribution en Finlande dans les dernières décennies et est considéré près de l'extinction dans le nord du pays (Hokkanen et al. 1982). Le déclin est associé à la perte d'habitat de forêts matures mixtes d'épinettes de Norvège (*Picea abies*)-feuillus ainsi qu'à la fragmentation du paysage par les coupes forestières (Hokkanen et al. 1982; Reunanen et al. 2000). Dans ce paysage, le polatouche occupe les fragments d'habitats ayant une plus grande superficie, un volume d'épinettes ainsi que de tremble plus important, plus de bois mort, une quantité supérieure d'habitat de qualité dans un rayon de 500 m aux alentours et une quantité inférieure d'habitat ouvert dans rayon de 200 m à 2 km (Mönkkönen et al. 1997; Reunanen et al. 2000, 2002; Hurme et al. 2005; Hurme et al. 2007; Hurme et al. 2008). Le pourcentage d'habitat ouvert dans un rayon de 1 km est négativement corrélé à la présence de l'espèce et ce facteur à lui seul permet de prédire 75% des sites occupés (Mönkkönen et al. 1997). De plus, les habitats occupés sont distribués en grappes et sont connectés aux autres fragments de façon plus importante que les sites non occupés, ce qui suggère que la connectivité est nécessaire au maintien de l'espèce (Reunanen et al. 2000; Hurme et al. 2007). La persistance des populations de Grand Polatouche dans les habitats fragmentés dépend de la capacité de cette espèce à se déplacer à travers le paysage. D'après D'Eon et al. (2002), le Grand Polatouche serait une espèce particulièrement à risque avec la plus faible capacité de dispersion (médiane 430 m, max 4.9 km) parmi les 18 espèces associées aux vieilles forêts qu'ils ont étudiées en Colombie-Britannique. Ces résultats suggèrent que la connectivité est essentielle au maintien de l'espèce (Weigl 2007).

Objectif général

En forêt boréale mixte de l'est du Canada, il a été suggéré que la disponibilité des cavités soit naturellement faible et que la taille relativement grande du polatouche le rende susceptible d'être limité par la disponibilité des cavités, particulièrement en période froide. Les objectifs de ce projet sont de décrire l'utilisation de l'habitat par le Grand Polatouche à diverses échelles et de déterminer l'importance des cavités en période hivernale dans une partie de son aire de répartition où les cavités sont naturellement peu abondantes. En effet, la région de l'Abitibi-Témiscamingue (47°46' à 49°00' N; 79°53' à 78°22'W) possède trois caractéristiques qui en font une région intéressante pour cette étude. Tout d'abord, les essences dominantes dans cette zone (Épinette noire (*Picea mariana*), Pin gris (*Pinus banksiana*), Peuplier faux-tremble (*Populus tremuloides*) et Bouleau blanc (*Betula papyrifera*)) atteignent rarement un large diamètre à hauteur de poitrine (dhp $\geq$ 25-30 cm) qui est essentiel à la formation de grandes cavités. Ensuite, la forêt est dominée majoritairement par des conifères qui sont moins enclins que les feuillus à former des cavités en cassant des branches. Finalement, l'excavateur principal de grandes cavités, le Grand Pic (*Dryocopus pileatus*), est présent en faible densité puisqu'il y atteint la limite nord de sa distribution en Amérique du Nord.

Le présent projet comporte trois volets avec des méthodes complémentaires. Le premier volet tente de relier la présence du Grand Polatouche aux caractéristiques du paysage. Il a été réalisé en visitant un réseau de nichoirs à nyctales (*Aegolius sp*) installés en 2003. L'occupation des nichoirs par le Grand Polatouche a été reliée aux caractéristiques du paysage à l'aide des attributs disponibles répertoriés sur les cartes écoforestières de la région. Le deuxième volet tente de déterminer l'utilisation des cavités par le Grand Polatouche à l'échelle du domaine vital. Des sessions de piégeage ont été réalisées dans des peuplements de Peuplier faux-tremble d'âge variable pour déterminer la présence du Grand Polatouche en fonction des attributs de l'habitat. Finalement, le troisième volet se rattache à l'échelle du nid. Une quarantaine d'individus ont été munis de colliers émetteurs et localisés par télémétrie à leur refuge diurne pour décrire les caractéristiques spécifiques des arbres à nids utilisés. Malgré que le Grand Polatouche ait déjà fait l'objet de plusieurs études, il n'existe que peu de connaissances sur l'utilisation de l'habitat par cette espèce dans les régions froides de son

aire de répartition où la température hivernale pourrait imposer une contrainte sur le choix de la structure de nid utilisée. Cette étude permettra de vérifier si la disponibilité de cavités peut représenter un facteur limitant pour le Grand Polatouche, particulièrement en période froide.

ARTICLE I

THE USE OF NEST BOXES TO ASSESS WINTER HABITAT USE BY THE NORTHERN FLYING SQUIRREL IN BOREAL MIXEDWOODS OF NORTHWESTERN QUEBEC

The use of nest boxes to assess winter habitat use by the northern flying squirrel in boreal mixedwoods of northwestern Quebec

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Abstract

We assessed winter habitat use by the northern flying squirrel to test the hypothesis that the species is not a late-seral coniferous forest specialist in boreal mixedwood forests of northwestern Quebec. We monitored 149 pairs of nest boxes over three visits during February-April 2008, of which a total of 31 pairs of nest boxes were occupied during the study. The average (3.7, 2.8, and 1.8) and maximum (8, 6, and 4) numbers of individuals in nest boxes decreased from the first to last visit. Average air temperatures were below freezing and increased with the arrival of spring (-23.9, -14.5, and -3.7°C). Using GIS software, we created a 430-m (median dispersal distance) buffer around each pair of nest boxes and extracted habitat variables describing landscape composition from digital forest inventory maps. We created models that potentially explained site occupancy by the northern flying squirrel as well as detection probability. Model selection indicated that the proportion of coniferous forests negatively affected site occupancy by flying squirrels while temperature positively influenced detection probability. Our results support the hypothesis that the northern flying squirrel is not a habitat specialist, but can occupy a wider range of habitats than previously recognized.

Résumé

Nous avons étudié l'utilisation hivernale de l'habitat par le Grand Polatouche afin de tester l'hypothèse que l'espèce n'est pas spécialiste des vieilles forêts de conifères dans la forêt boréale mixte du nord-ouest du Québec. Nous avons visité 149 paires de nichoirs à trois reprises entre février - avril 2008, et obtenu un total de 31 paires de nichoirs occupées pendant l'étude. Le nombre d'individus moyen (3.7, 2.8, et 1.8) et maximum (8, 6, and 4) dans les nichoirs a diminué de la première à la dernière visite. Les températures moyennes étaient sous le point de congélation et elles ont augmenté avec l'arrivée du printemps (-23.9, -14.5, and -3.7°C). En utilisant un SIG, nous avons créé une zone tampon de 430-m (distance de dispersion médiane) autour de chaque paire de nichoirs pour ensuite extraire des cartes écoforestières plusieurs variables d'habitat décrivant la composition du paysage. Nous avons créé des modèles pouvant expliquer l'occupation de site par le Grand Polatouche et la probabilité de détection. La sélection de modèle a montré que la proportion de forêt de conifères affectait négativement l'occupation de site par le Grand Polatouche, alors que l'augmentation de la température influençait positivement la probabilité de détection. Nos résultats supportent l'hypothèse que le Grand Polatouche n'est pas un spécialiste dans l'utilisation de l'habitat mais qu'il est capable d'occuper une plus grande variété de milieux que ce qui était reconnu.

Key words: *Glaucomys sabrinus,* cavities, cold, GIS and site occupancy.

Introduction

The northern flying squirrel, *Glaucomys sabrinus* (Shaw, 1801), is a nocturnal arboreal rodent common across forested landscapes of northern North America (Wells-Gosling and Heaney 1984). As the main prey item of the northern spotted owl (*Strix occidentalis caurina* (Merriam, 1898)) in the Pacific Northwest, it has been largely studied in this region and its optimal habitat is described as old-growth coniferous forest (Carey 1991, 1995; Witt 1992; Smith and Nichols 2003). This selection is explained by its important consumption of truffles, i.e., hypogeous fruiting bodies (Maser et al. 1986; Pyare et al. 2002; Lehmkuhl et al. 2004), of ectomycorrhizal fungi associated with the roots of conifers in the Pinaceae (Maser and Maser 1988) and by its use of tree cavities (Smith 2007). In the Appalachians, northern flying squirrel habitat has also been defined as coniferous-dominated forest at high elevation or conifer-hardwood ecotones (Weigl et al. 1992; Odom et al. 2001; Menzel et al. 2006). However, recent studies in continental regions suggest that this species is less specialized in its habitat use than previously expected, as shown by its presence in mixed or deciduous forests (Wheatley et al. 2005; Holloway 2006), and in residual stands fragmented after logging (Bayne and Hobson 1998; Côté and Ferron 2001).

Few studies have examined the habitat characteristics of the northern flying squirrel in the northern part of its range, particularly in the boreal forest. As this region is characterized by a continental climate with average temperatures below freezing for five to six months per year, a considerable energetic demand is imposed on small mammals, including the northern flying squirrel, which is active year-round. It is generally recognized that cavities represent better winter nest choices than do external nests (Wells-Gosling and Heaney 1984), as the former offers better protection from precipitation, wind, and cold temperatures. Flying squirrels are also known to aggregate in nests (Mowrey and Zasada 1984; Gerrow 1996), and thus, large cavities are necessary for cohabitation. Availability of suitable cavities has been proposed as a factor limiting this species (Smith 2007). When available, nest boxes are readily used by flying squirrels (Maser et al. 1981; Carey 2002; Ransome and Sullivan 2004). As such, nest boxes may represent an effective way to assess site occupancy and habitat use (Fokidis and Risch 2005).

In this study, our main objective was to investigate habitat use by the northern flying squirrel in boreal mixedwood forests using nest boxes during winter. Since cavity availability is an important limiting factor for the northern flying squirrel (Carey 2002), that most cavities in the boreal forest are excavated by woodpeckers rather than of natural origin (Aitken and Martin 2007), and that cavities are mainly excavated in trunks of trembling aspen (*Populus tremuloides* Michaux) in boreal mixedwood forests (Drapeau et al. 2009), we hypothesized that the flying squirrel is not associated with coniferous forest cover types in our study area but instead inhabits a wide range of forest cover types that include trembling aspen. Thus, we predicted that the proportion of deciduous and mixedwood forests in the landscape would positively affect nest box use as they provide abundant nest sites in our study area relative to stands dominated by coniferous forest cover. Large trees have also been associated with the presence of the northern flying squirrel in the boreal forest (McDonald 1995) and we expected that nest boxes surrounded by mature and older forests would be occupied. We also expected that open habitats in the landscape would negatively affect nest box use because they limit movement and dispersal of flying squirrels (Bendel and Gates 1987). Like cavities, nest boxes provide shelter from inclement weather. Consequently, we expected that decreasing temperature would positively affect nest box use.

Materials and methods

Study area

The study took place in the boreal mixedwood forest of northwestern Quebec (47°46' - 49°00'N, 79°53' - 78°22'W), which is located on the northern Clay Belt and characterized by clay soils and low rocky hills. Mean annual temperature is 1°C and average annual precipitation is 914 mm (Environment Canada 2009). This region is part of the balsam fir-white birch bioclimatic domain of the boreal forest (Robitaille and Saucier 1998), and consists of trembling aspen, balsam poplar (*Populus balsamifera* L.), white or paper birch (*Betula papyrifera* Marsh.), white spruce (*Picea glauca* (Voss) Moench), black spruce (*Picea mariana* (Mill.) BSP), jack pine (*Pinus banksiana* Lamb.), and balsam fir (*Abies balsamea* (L.) Mill.). The landscape is characterized by a mixture of coniferous, mixed, and deciduous forests interspersed with agricultural fields and clear-cuts, as well as numerous lakes and rivers.

Nest boxes

We monitored a network of 149 pairs of nest boxes that were installed in 2003 for northern saw-whet owl (*Aegolius acadicus (Gmelin, 1788)*) and boreal owl (*Aegolius funereus (Linnaeus, 1758)*) nesting but these were also used as winter shelter by northern flying squirrels. The location of each nest box pair was determined using a stratified sampling design to ensure adequate representation of the variation in forest cover occurring over the region (mean = 77%, range = 26 - 100% forest in 430-m buffer), as well as existing forest cover types (coniferous, mixed, and deciduous). The nest boxes (19.8 × 19.8 × 44 cm height; 7.15 cm dia. entrance) were handmade with ca. 1.5 cm thick plywood and designed with a side door to access the interior. They were installed at a 4-m height on a dominant tree and the bottom of the boxes was covered with wood chips to encourage bird nesting. Nest boxes were distributed along roads with an average distance of 20 m between the nest boxes of a pair and three km between each pair.

Each pair of nest boxes was visited three times during winter and early spring 2008 (between February 14th and April 12th) to determine the presence and number of northern flying squirrels. As this species is strictly nocturnal (Cotton and Parker 2000), the nest boxes were visited at any time of the day except 30 minutes after sunrise or before sunset to ensure that nests were being used at the time of checking. Using a ladder, each nest box was inspected for northern flying squirrels following the same procedure: 1) a few knocks were given on the door; 2) the door was opened; 3) if it contained a squirrel's nest, the latter was shaken; and finally, 4) the nest was inspected to ensure that no individual was missed. This exercise was performed with a second observer on the ground with an unobstructed view of the nest box entrance. This observer was able to count flying squirrels coming out of the nest box. All 149 nest box pairs were checked during the first visit. However, 2 and 14 pairs could not be checked during the second and third visits, respectively, due to difficult access and warmer weather affecting snow conditions.

Habitat and environmental variables

We determined which factors influenced nest box use by the northern flying squirrel using different habitat variables describing landscape composition (Table 1). The variables were chosen in order to assess specialization of flying squirrel habitat use in terms of forest

composition (conifer versus deciduous tree cover) and developmental stages (greater than 7 or 12 m in height). These variables were extracted using ArcView® 3.2 (ESRI 1999) from 1995 digitized forest cover maps (1:20000 scale) that were produced by the Ministère des Ressources naturelles et de la Faune du Québec (MRNF) and which were updated with recent clear-cuts (1993-2007). We created a 430-m buffer around each pair of nest boxes and extracted areas corresponding to each variable within the buffer. This buffer value was chosen as it represents the median dispersal distance for flying squirrels (D'Eon et al. 2002).

We also tested the impact of temperature on nest box use by flying squirrels. We used the minimal temperature between 0:00 and 6:00 on the day of observation. All data were acquired from the closest meteorological station, which was located in the city of Val-d'Or (48° 03'N, 77°47'W), and downloaded from the Environment Canada website (Environment Canada 2009).

Statistical analysis

We analyzed flying squirrel presence at nest boxes using single season occupancy models from program PRESENCE 2.4 (Hines 2006; MacKenzie et al. 2006). To account for false absences, this method estimates a probability of detection using data from repeated visits (MacKenzie et al. 2002). Each nest box pair was considered as an independent site. On a given visit, each nest box pair contributed a single binary observation: squirrels were either detected or not at each site. All variables were centered prior to analysis. Strong correlations ($r \geq 0.7$) occurred among certain habitat variables. To avoid including highly correlated variables in the same models, we considered a set of 23 models to explain the presence of the northern flying squirrel at our sites and included variables known to affect the use of nest boxes based on the scientific literature. All models included habitat variables as well as temperature and visit. We tested the fit of each of ten global models to the data by using a parametric bootstrap approach with 10000 bootstrap samples ($\hat{c} > 1.0$ indicated overdispersion of the data). We used Akaike's Information Criterion, adjusted for small sample size (i.e., total number of sites), to compare candidate models (Burnham and Anderson 2002). We considered models with ΔAICc values ≤ 2 to have strong support and we also calculated model probabilities from the AICc values to indicate the level of support for each model considered (Burnham and Anderson 2002). We used R software version 2.9.2

(R Development Core Team 2009) to program and implement multimodel inference to assess the effect of variables on either occupancy or detection probability.

Results

A total of 31 pairs of nest boxes were occupied over the three visits, with fewer pairs occupied during the first (12) and second (17) visits compared to the third (25). The average number of flying squirrels in occupied pairs was 2.8 per nest box over the three visits, with more individuals observed during the first (3.7) and second (2.8) visits compared to the third (1.8). We also observed an aggregation of 8 flying squirrels in a nest box during the first visit, while the maximum numbers of individuals in subsequent visits were 6 (second visit) and 4 (third visit) animals, respectively. The mean temperature over the three visits was − 4.3°C; consistent with expectation, average air temperature increased as the season progressed, from - 23.9°C on the first visit to - 14.5°C on the second visit, and to - 3.7°C on the third.

None of the 10 global models in our candidate model set suggested overdispersion in the data as ĉ was equal to 1. A single model had strong support from the site occupancy analysis with an Akaike weight of 0.83 (Table 2) and it included the variables conifer cover (Coniferous) on occupancy and minimal air temperature (Temperature) on detection. This model was 10 times more likely than the second-ranked model, which consisted of conifer cover on occupancy and time on detection. The proportion of coniferous habitat surrounding each pair of nest boxes negatively affected the probability of site occupancy (model-averaged β = − 0.10, 95% CI = - 0.05, - 0.15; Fig. 1). As for detection probability, it was positively affected by temperature (model-averaged β = 0.07, 95% CI = 0.03, 0.12; Fig. 2).

Discussion

Our results support recent studies suggesting that the northern flying squirrel is not a coniferous forest specialist and can use a wider variety of habitats than previously thought (Wheatley et al. 2005; Holloway 2006). Nest box occupancy was negatively related to the proportion of coniferous habitat within a 430-m buffer, but there were no effects of stand age or open habitats. This indirectly supports our hypothesis that deciduous and mixedwood

forests are important habitat for this species. Indeed, flying squirrels used nest boxes surrounded by deciduous or mixed forest habitats and avoided coniferous stands, reflecting the importance of deciduous trees, particularly trembling aspen, in their habitat use. The absence of an effect of mature forest or open habitats also suggests that flying squirrels can use various habitat types.

We acknowledge that our methodology chosen to determine and explain site occupancy by northern flying squirrels has some potential biases. In a companion study conducted in different sites, we showed that external or ground nests were more likely to be used than cavities in cold temperature (Trudeau, C., Imbeau L., Drapeau, P. and Mazerolle, M.J., *in review*) and this might be explained by differences in thermal insulation value or sharing capacity. Because nest availability may differ between sites (i.e. cavities excavated in deciduous trees and external nests built in conifers), it has the potential to influence the appeal of nest boxes to northern flying squirrels. However, we believe that this difference is negligible because ground nests are available everywhere and most deciduous stands have some conifers in which to install an external nest. Another consideration about methodology is the validity of digitized forest cover maps. Field validation showed that cover type and dominant tree species was correctly identified for jack pine and black spruce stands on the maps in our region while agreement was poor for mixed and deciduous stands, although height classes were generally accurate (Potvin et al. 1999). Consequently, we limited our stand variables to cover types defined by height classes.

Site occupancy by northern flying squirrels was negatively influenced by the proportion of coniferous forest surrounding each nest box. This result differs from a study conducted by Wheatley et al. (2005) in mixedwood forests of the boreal plain of Alberta, where no relationship were found between squirrel abundance and conifer-dominance in stand composition, stand age, or non-forested openings at the landscape scale (50-, 150- and 300-m) using data from digital map inventories. These authors did capture flying squirrels in all of the habitats that they had sampled (coniferous, mixed, and deciduous stands). Our findings corroborated their conclusions, however, that flying squirrel populations do not seem to be associated with old-aged or conifer forests. In contrast, McDonald (1995) observed a positive relationship between flying squirrel abundance and density of white spruce in aspen

mixedwood forests of Alberta, but all of the stands that she selected had > 80% aspen canopy cover.

It is recognized that the northern flying squirrel consumes both truffles and aboveground fungal sporocarps in boreal mixedwood forests (Currah et al. 2000; Wheatley 2007) and that ectomycorrhizal fungi, especially those producing truffles, are mostly symbiotic with the roots of conifers (Maser and Maser 1988). Therefore, conifers may be associated with a high abundance of food for the northern flying squirrel at the microhabitat scale (Pyare and Longland 2002). Aspen also exhibits an ectomycorrhizal habit, but it tends to associate with mycobionts that produce epigeous (aboveground) sporocarps (Cripps 2001) and rarely, if ever, forms associations with genera that produce hypogeous (belowground) fruiting bodies, such as the truffle-forming *Rhizopogon* (Godbout and Fortin 1985) or *Tuber* (Visser et al. 1998). Even though the northern flying squirrel might require conifers to gain access to food resources in certain regions, in our study area they inhabit deciduous and mixed forests of the boreal mixedwoods and avoid purely coniferous landscapes.

There was no effect of the proportion of mature and older forests in the landscape on site occupancy. In Alberta, northern flying squirrels were more abundant in old stands than younger stands (McDonald 1995). However, old stands (> 120 years) represented only 1.5% of the total area considered for the analysis of our 149 sites. Our sites (10-90 years) were comparable to the stands considered as mature (50-70 years) or young (< 30 years) in the Alberta study, which had medium to low abundance of flying squirrels. It is possible that the characteristics associated with old-growth forests, and which are of interest to northern flying squirrels, such as abundant cavities and highly decomposed woody debris used as growth substrates for fungi, were not encountered in our study area.

Contrary to our hypothesis, we observed a positive effect of temperature on detection probability. This is not surprising as the range of temperature was shown to be on average 6.5°C colder inside nest boxes than inside cavities in a bottomland hardwood stand in Louisiana (McComb and Noble 1981). Thus, the thermal insulation of a nest box might not be sufficient for winter use by the northern flying squirrel in the boreal forest. In fact, nest box use increased from the first to the third visit (12, 17 and 25 occupied pairs) with

increasing air temperature (-23.9°C, -14.5°C and -3.7°C). An alternative to compensating for the low insulation value of nests is to cohabitate with other individuals. Northern flying squirrels have been shown to aggregate in nests after a sharp drop in temperature (Mowrey and Zasada 1984; Gerrow 1996; Cotton and Parker 2000); moreover, such aggregations have been shown to reduce energy expenditure up to 33% in southern flying squirrels (Stapp et al. 1991). Interestingly, we recorded the maximum number of flying squirrels that were observed to be sharing a nest box during the first visit, which was also the coldest. This would also affect detection probability as fewer nests are used during the cold winter period due to aggregations, limiting the probability of a nest box to be used by at least one squirrel. Flying squirrels could either prefer other nest types in cold weather and only use nest boxes in warmer temperature, or aggregate in nest boxes when the temperature is colder, which would also limit detection success.

The increase in temperature also coincided with the arrival of spring and the breeding period. Reproductive females have been shown to choose cavities during the breeding period in the Pacific Northwest (Carey et al. 1997), in central Ontario (Holloway and Malcolm 2007), and in New Brunswick (Gerrow 1996). Nest boxes are also used by reproductive females (Ransome and Sullivan 2004) as a substitute for cavities when the latter are not available. However, we do not believe that reproductive females were the cause of increased detection probability with increasing temperature. Nest boxes are monitored in the spring and summer for nesting by northern saw-whet and boreal owls, but no reproductive female northern flying squirrels with young have subsequently been recorded in 2008. Indeed, only 4 nest boxes were still used by flying squirrels after May 1st 2008 (J. Gagnon, *personal communication* 2010). Therefore, the arrival of spring and the reproductive period is not an alternative explanation for the effect of temperature on detection probability.

In conclusion, this exploratory analysis supports the hypothesis that the northern flying squirrel is not associated with late-seral coniferous forests in the boreal mixedwood forest of eastern Canada and that it can use a wider variety of habitats than previously recognized. Even though conifers provide a fine-scale food resource, deciduous and mixed forests can represent a suitable habitat for this species and are preferable to coniferous forests. We showed that temperature affects nest box use, and we suggest that this variable should be

taken into consideration with appropriate methods when site occupancy is the state variable of interest.

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References

Aitken, K.E.H., and Martin, K. 2007. The importance of excavators in hole-nesting communities: availability and use of natural tree holes in old mixed forests of western Canada. J. Ornithol. **148**: S425-S434. doi:10.1007/s10336-007-0166-9.

Bayne, E.M., and Hobson, K.A. 1998. The effects of habitat fragmentation by forestry and agriculture on the abundance of small mammals in the southern boreal mixedwood forest. Can. J. Zool. **76**(1): 62-69. doi:10.1139/cjz-76-1-62.

Bendel, P.R., and Gates, J.E. 1987. Home range and microhabitat partitioning of the southern flying squirrel (*Glaucomys volans*). J. Mammal **68**(2): 243-255.

Burnham, K.P., and Anderson, D.R. 2002. Model selection and multimodel inference: a practical information-theoretic approach. 2nd ed. Springer-Verlag, New York, NY.

Carey, A.B. 1991. The biology of arboreal rodents in Douglas-fir forests. Forest Service General Technical Report PNW-GTR-276, Pacific Northwest Research Station, United States Department of Agriculture, Olympia, Washington.

Carey, A.B. 1995. Sciurids in Pacific Northwest managed and old-growth forests. Ecol. Appl. **5**(3): 648-661. doi:10.2307/1941974.

Carey, A.B. 2002. Response of northern flying squirrels to supplementary dens. Wildl. Soc. Bull. **30**(2): 547-556.

Carey, A.B., Wilson, T.M., Maguire, C.C., and Biswell, B.L. 1997. Dens of northern flying squirrels in the Pacific Northwest. J. Wildl. Manage. **61**(3): 684-699.

Côté, M., and Ferron, J. 2001. Short-term use of different residual forest structures by three sciurid species in a clear-cut boreal landscape. Can. J. For. Res. **31**(10): 1805-1815. doi:10.1139/cjfr-31-10-1805.

Cotton, C.L., and Parker, K.L. 2000. Winter activity patterns of northern flying squirrels in sub-boreal forests. Can. J. Zool. **78**(11): 1896-1901. doi:10.1139/cjz-78-11-1896.

Cripps, C.L. 2001. Mycorrhizal fungi of aspen forests: Natural occurrence and potential applications. *In* Sustaining aspen in western landscapes: symposium proceedings, 13-15 June 2000, Grand Junction, CO. *Compiled by* W.D. Shepperd, D. Binkley, D.L. Bartos, T.J. Stohlgren, and L.G. Eskew. USDA Forest Service, Fort Collins, CO. Proceedings RMRS-P-18. pp. 285-298.

Currah, R.S., Smreciu, E.A., Lehesvirta, T., Niemi, M., and Larsen, K.W. 2000. Fungi in the winter diets of northern flying squirrels and red squirrels in the boreal mixedwood forest of northeastern Alberta. Can. J. Bot. **78**(12): 1514-1520. doi:10.1139/cjb-78-12-1514.

D'Eon, R.G., Glenn, S.M., Parfitt, I., and Fortin, M.-J. 2002. Landscape connectivity as a function of scale and organism vagility in a real forested landscape. Conserv. Ecol. **6**(2): 10. Available from www.consecol.org/vol6/iss2/art10 [accessed 10 June 2008].

Drapeau, P., Nappi, A., Imbeau, L., and Saint-Germain, M. 2009. Standing deadwood for keystone bird species in the eastern boreal forest: Managing for snag dynamics. Forest Chron. **85**(2): 227-234.

Environment Canada. 2009. Canadian Climate Normals 1971-2000 [online]. Available from climate.weatheroffice.ec.gc.ca [accessed 14 December 2009].

ESRI. 1999. ArcView® GIS. Environmental Systems Research Institute, Inc., Redlands, CA.

Fokidis, H.B., and Risch, T.S. 2005. The use of nest boxes to sample arboreal vertebrates. Southeast. Nat. **4**(3): 447-458. doi:10.1656/1528-7092(2005)004[0447:TUONBT]2.0.CO;2.

Gerrow, J.S. 1996. Home range, habitat use, nesting ecology and diet of the northern flying squirrel in southern New Brunswick. M.Sc. thesis, Acadia University, Wolfville, NS.

Godbout, C., and Fortin, J.A. 1985. Synthesized ectomycorrhizae of aspen: fungal genus level of structural characterization. Can. J. Bot. **63**(2): 252-262. doi: 10.1139/b85-029.

Hines, J.E. 2006. PRESENCE2- Software to estimate patch occupancy and related parameters [online]. Available from mbr-pwrc.usgs.gov/software/presence.html [accessed 5 October 2009].

Holloway, G.L. 2006. Flying squirrel (*Glaucomys sabrinus* and *G. volans*) habitat use and ecology in landscapes managed with partial harvesting silviculture in central Ontario. Ph.D. dissertation, University of Toronto, Toronto, ON.

Holloway, G.L., and Malcolm, J.R. 2007. Nest-tree use by northern and southern flying squirrels in central Ontario. J. Mammal. **88**(1): 226-233. doi:10.1644/05-MAMM-A-368R2.1.

Lehmkuhl, J.F., Gould, L.E., Cázares, E., and Hosford, D.R. 2004. Truffle abundance and mycophagy by northern flying squirrels in eastern Washington forests. For. Ecol. Manag. **200**(1-3): 49-65.

MacKenzie, D.I., Nichols, J.D., Lachman, G.B., Droege, S., Royle, J.A., and Langtimm, C.A. 2002. Estimating site occupancy rates when detection probabilities are less than one. Ecology **83**(8): 2248-2255. doi:10.1890/0012-9658(2002)083[2248:esorwd]2.0.co;2.

MacKenzie, D.I., Nichols, J.D., Royle, J.A., Pollock, K.H., Bailey, L.L., and Hines, J.E. 2006. Occupancy estimation and modeling - inferring patterns and dynamics of species occurrence. Academic Press, New York, NY.

Maser, C., Anderson, R., and Bull, E.L. 1981. Aggregation and sex segregation in northern flying squirrels in northeastern Oregon, an observation. Murrelet, **62**(2): 54-55.

Maser, C., and Maser, Z. 1988. Interactions among squirrels, mycorrhizal fungi, and coniferous forests in Oregon. Great Basin Nat. **48**(3): 358-369.

Maser, C., Maser, Z., Witt, J.W., and Hunt, G. 1986. The northern flying squirrel: a mycophagist in southwestern Oregon. Can. J. Zool **64**(10): 2086-2089. doi:10.1139/z86-318.

McComb, W.C., and Noble, R.E. 1981. Microclimate of nest boxes and natural cavities in bottomland hardwoods. J. Wildl. Manage. **45**(1): 284-289.

McDonald, L. 1995. Relationships between northern flying squirrels and stand age and structure in aspen mixedwood forests in Alberta. *In* Relationships between stand age, stand structure, and biodiversity in aspen mixedwood forests in Alberta. *Edited by* J.B.

Stelfox. Jointly published by Alberta Environmental Centre (AECV95-R1), Vegreville, AB, and Canadian Forest Service (Project No. 0001A), Edmonton, AB. pp. 227-240.

Menzel, J.M., Ford, W.M., Edwards, J.W., and Terry, T.M. 2006. Home range and habitat use of the Vulnerable Virginia northern flying squirrel *Glaucomys sabrinus fuscus* in the Central Appalachian Mountains, USA. Oryx **40**(2): 204-210. doi:10.1017/S0030605306000494.

Mowrey, R.A., and Zasada, J.C. 1984. Den tree use and movements of northern flying squirrels in interior Alaska and implications for forest management. *In* Fish and wildlife relationships in old-growth forests: proceedings of a symposium, Juneau, Alaska, 12-15 April, 1982. *Edited by* W.R. Mechan, T.R. Merrell Jr., and T.A. Hanley. American Institute of Fishery Research Biologists, Juneau, AK. pp. 351-356.

Odom, R.H., Ford, W.M., Edwards, J.W., Stihler, C.W., and Menzel, J.M. 2001. Developing a habitat model for the endangered Virginia northern flying squirrel (*Glaucomys sabrinus fuscus*) in the Allegheny Mountains of West Virginia. Biol. Conserv. **99**(2): 245-252.

Pyare, S., and Longland, W.S. 2002. Interrelationships among northern flying squirrels, truffles, and microhabitat structure in Sierra Nevada old-growth habitat. Can. J. For. Res. **32**(6): 1016-1024. doi:10.1139/x02-002.

Pyare, S., Smith, W.P., Nicholls, J.V., and Cook, J.A. 2002. Diets of northern flying squirrels, *Glaucomys sabrinus*, in southeast Alaska. Can. Field-Nat. **116**(1): 98-103.

R Development Core Team. 2009. R: A language and environment for statistical computing [online]. R Foundation for Statistical Computing, Vienna, Austria. ISBN 3-900051-07-0, Available from www.R-project.org [accessed 5 September 2009].

Ransome, D.B., and Sullivan, T.P. 2004. Effects of food and den-site supplementation on populations of *Glaucomys sabrinus* and *Tamiasciurus douglasii*. J. Mammal. **85**(2): 206-215. doi:10.1644/bos-118.

Robitaille, A., and Saucier, J.-P. 1998. Paysages régionaux du Québec méridional. Les publications du Québec, Sainte-Foy, QC.

Smith, W.P. 2007. Ecology of *Glaucomys sabrinus*: Habitat, demography, and community relations. J. Mammal. **88**(4): 862-881. doi:10.1644/06-mamm-s-371r1.1.

Smith, W.P., and Nichols, J.V. 2003. Demography of the Prince of Wales flying squirrel, an endemic of southeastern Alaska temperate rain forest. J. Mammal. **84**(3): 1044-1058. doi:10.1644/BBa-033.

Stapp, P., Pekins, P.J., and Mautz, W.W. 1991. Winter energy expenditure and the distribution of southern flying squirrels. Can. J. Zool. **69**(10): 2548-2555. doi:10.1139/z91-359.

Visser, S., Maynard D. and Danielson, R.M. 1998. Response of ecto- and arbuscular mycorrhizal fungi to clear-cutting and the application of chipped aspen wood in a mixedwood site in Alberta, Canada. Appl. Soil Ecol., **7**(3): 257-269. doi:10.1016/S0929-1393(97)00060-7.

Weigl, P.D., Knowles, T.W., and Boynton, A.C. 1992. The distribution and ecology of the northern flying squirrel, *Glaucomys sabrinus coloratus*, in the southern Appalachians. Nongame and Endangered Wildlife Program, North Carolina Wildlife Resources Commission, Raleigh, NC.

Wells-Gosling, N., and Heaney, L.R.. 1984. *Glaucomys sabrinus*. Mamm. Species, **229**: 1-8.

Wheatley, M. 2007. Fungi in summer diets of northern flying squirrels (*Glaucomys sabrinus*) within managed forests of western Alberta, Canada. Northwest Sci. **81**(4): 265-273. doi:10.3955/0029-344x-81.4.265.

Wheatley, M., Fisher, J.T., Larsen, K., Litke, J., and Boutin, S. 2005. Using GIS to relate small mammal abundance and landscape structure at multiple spatial extents: the northern flying squirrel in Alberta, Canada. J. Appl. Ecol. **42**(3): 577-586. doi:10.1111/j.1365-2664.2005.01034.x.

Witt, J.W. 1992. Home range and density estimates for the northern flying squirrel, Glaucomys sabrinus, in western Oregon. J. Mammal. **73**(4): 921-929.

Table 1. Description of the landscape composition variables extracted from digitized forestry maps. Values for mean area and range are expressed in hectares and calculated within the 430-m buffer of each site.

Variables	Description	Mean (Range)
Coniferous (Con)	Stands dominated by conifers (Coniferous or Mixed) > 7 m	17.3 (0-57.8)
Deciduous (Dec)	Stands dominated by deciduous trees (Deciduous or Mixed) > 7 m	21.8 (0-56.1)
Open	Open habitats including; forested stands <2 m, water, agricultural fields, fallows, deforested and urban areas	12.1 (0-42.7)
Forest (For)	All forested stands (Coniferous, Deciduous and Mixed) > 7 m	44.4 (15.1-57.8)
Mature (Mat)	All forested stands (Coniferous, Deciduous and Mixed) > 12 m	26.4 (0-53.5)
Mature Coniferous (MatCon)	Stands dominated by conifers (Coniferous or Mixed) > 12 m	8.9 (0-47.5)
Mature Deciduous (MatDec)	Stands dominated by deciduous trees (Deciduous or Mixed) > 12 m	17.5 (0-53.5)

Dominance is described as 50-75% of total basal area of the stand

Table 2. Model selection results for northern flying squirrel occupancy (ψ) and detection probability (*p*) in northwestern Québec, Canada, during winter and early spring 2008. Variable codes are described in Table 1.

Model	K[a]	AICc[b]	ΔAICc[c]	w_i[d]	Deviance[e]
ψ(Con), *p*(Temp)*	4	238.52	0.00	0.83	230.25
ψ(Con), *p*(Visit)*	5	243.12	4.60	0.08	232.71
ψ(MatCon), *p*(Temp)	4	244.44	5.92	0.04	236.16
ψ(MatCon+Open), *p*(Temp)	5	246.35	7.83	0.02	235.93
ψ(MatDec+MatCon+Open), *p*(Temp)*	6	246.64	8.12	0.01	234.05
ψ(Dec), *p*(Temp)*	4	247.52	9.00	0.01	239.24
ψ(MatCon), *p*(Visit)	5	248.85	10.33	0.00	238.43
ψ(MatCon+Open), *p*(Visit)	6	250.82	12.30	0.00	238.23
ψ(MatDec+MatCon+Open), *p*(Visit)*	7	251.26	12.74	0.00	236.46
ψ(Dec), *p*(Visit)*	5	251.93	13.41	0.00	241.51
ψ(MatDec+Open), *p*(Temp)	5	255.22	16.70	0.00	244.80
ψ(MatDec), *p*(Temp)	4	256.09	17.57	0.00	247.81
ψ(MatDec+Open), *p*(Visit)	6	259.63	21.11	0.00	247.04
ψ(MatDec), *p*(Visit)	5	260.31	21.79	0.00	249.89
ψ(For), *p*(Temp)*	4	266.13	27.61	0.00	257.85
ψ(Open), *p*(Temp)	4	266.49	27.97	0.00	258.22
ψ(Mat), *p*(Temp)	4	266.97	28.45	0.00	258.69
ψ(Mat+Open), *p*(Temp)*	5	268.10	29.58	0.00	257.69
ψ(For), *p*(Visit)*	5	270.00	31.48	0.00	259.58
ψ(Open), *p*(Visit)	5	270.35	31.83	0.00	259.93
ψ(Mat), *p*(Visit)	5	270.80	32.28	0.00	260.38
ψ(Mat+Open), *p*(Visit)*	6	272.02	33.50	0.00	259.43
ψ(.), *p*(.)	2	275.84	37.32	0.00	271.76

[a] K = no. of parameters.

[b] AIC_c = Akaike's Information Criterion, corrected for small sample sizes.

[c] ΔAIC_c = AIC_c relative to the most parsimonious model.

[d] w_i = AIC_c model weight.

[e] deviance = -2×log-likelihood.

* = Global models.

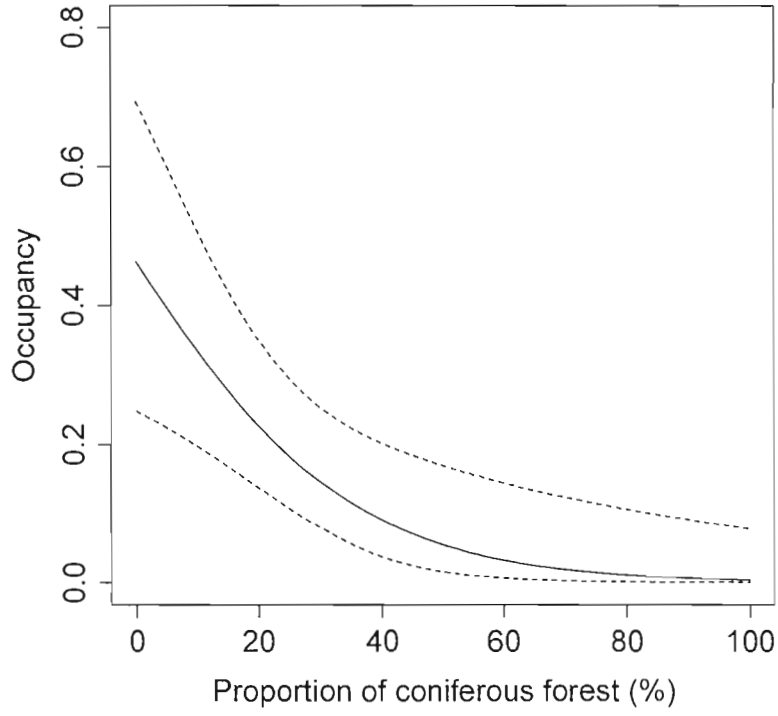

Figure 1. Effect of the proportion of coniferous forest on occupancy of nest boxes by northern flying squirrels in northwestern Québec, Canada, during winter and early spring 2008. Results are based on model-averaged predictions. Proportions are calculated within 430-m buffers. Dashed lines indicate 95% confidence limits.

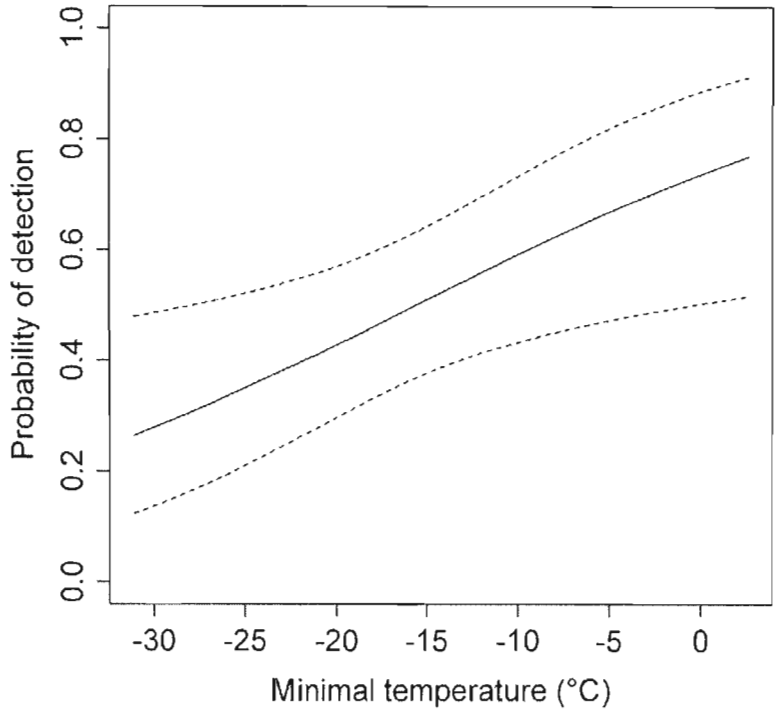

Figure 2. Effect of minimal temperature on detection probability of northern flying squirrels at nest boxes in northwestern Québec, Canada, during winter and early spring 2008. Results are based on model-averaged predictions. Error bars indicate 95% confidence limits.

ARTICLE II

IS THE NORTHERN FLYING SQUIRREL CAVITY-DEPENDENT DURING COLD MONTHS IN THE BOREAL FOREST?

Is the northern flying squirrel cavity-dependent during cold months in the boreal forest?

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Abstract

We assessed factors affecting site occupancy by northern flying squirrels to determine if cavities are an important resource, and to identify nest choice when air temperatures decrease in the boreal mixedwood forest of northwestern Québec during autumn-winter period of 2008-2009. We trapped flying squirrels twice in 59 aspen-dominated stands in the autumn using low- (1.5 - m above ground-level) and high-mounted (4 - m) traps to determine site occupancy. A total of 85 individuals were captured on 2880 trap-nights. During the winter, we radio-tracked 26 individuals to 90 different diurnal nests in 225 localizations. None of the habitat variables considered (cavity availability, woody debris and lateral cover) explained site occupancy. Detectability was influenced negatively by precipitation, was lower using high traps than low traps, and lower during the second visit than the first. However, uncertainty associated with model-averaged predictions was high. Both females and males used cavities (26%), external nests (39%), and ground nests (35%). In cold weather, females chose ground nests, whereas males seemed to chose external nests. Our results do not support the hypothesis that cavities represent a limiting factor to northern flying squirrels in cold environments. Instead, this species seems to be generalist and is opportunistic, using a variety of nest types.

Résumé

Nous avons étudié les facteurs qui affectent l'occupation de site par le Grand Polatouche pour déterminer si les cavités sont une ressource importante, et aussi identifier les nids choisies lorsque les températures baissent en forêt boréale mixte du nord-ouest du Québec pendant l'automne-hiver 2008-2009. À l'automne, nous avons piégé le Grand Polatouche à deux reprises dans 59 sites à dominance de peuplier faux-tremble en utilisant des pièges bas (1.5 - m) et hauts (4 - m) pour déterminer l'occupation de sites. Un total de 85 individus ont été capturés en 2880 nuits-pièges. Pendant l'hiver, nous avons localisé 90 nids diurnes différents en 225 localisations en effectuant le suivi télémétrique de 26 individus. Aucune des variables d'habitat considérées (disponibilité de cavité, débris ligneux et couvert latéral) n'expliquait l'occupation de site. La probabilité de détection était influencée négativement par les précipitations, était plus basse dans les pièges hauts que les pièges bas et était plus basse pendant la seconde visite que la première. Par contre, l'incertitude associée aux valeurs prédites pondérées par les modèles était élevée. Les femelles et les mâles utilisaient les cavités (26%), les nids externes (39%) et les nids au sol (35%). En période froide, les femelles préféraient les nids au sol, alors que les mâles semblaient préférer les nids externes. Nos résultats ne supportent pas l'hypothèse que les cavités représentent un facteur limitant pour le Grand Polatouche dans un climat rigoureux. Au contraire, cette espèce semble être généraliste et opportuniste, utilisant une variété de types de nids.

Key words: *Glaucomys sabrinus*, nest, trapping, telemetry and site occupancy.

Introduction

Cavities are used as shelter and breeding nests by numerous avian and mammalian species. As such, they represent a critical resource around which cavity-nesting communities are structured in nest webs (Martin and Eadie 1999). These nest webs are hierarchical networks, which consist of excavators that create the resource and secondary users that rely on available cavities (Martin et al. 2004, Blanc and Walters 2008). Creation of cavities also occurs to a lesser extent through natural processes such as wood decay, whereas loss is achieved through deterioration, resealing, and tree fall (Sedgwick and Knopf 1992). Thus, cavity availability is influenced by many factors including the rates of creation, cavity reuse by excavators, and loss, together with territoriality and competition among cavity-nesters (Aitken et al. 2002). As secondary users must use existing cavities for reproduction, cavity availability represents a key element which has the potential to limit their population size (Newton 1994).

The northern flying squirrel, *Glaucomys sabrinus* (Shaw, 1801), is a secondary user of cavities and is common across forested regions of North America. Its distribution ranges from Alaska to California, through central Canada and extends to North Carolina (Wells-Gosling and Heaney 1984). Until recently, the northern flying squirrel was reputed to be a late-seral coniferous forest specialist associated with legacies such as large trees, large snags, and coarse woody debris (Carey 1995; Gerrow 1996; Carey et al. 1999). This habitat selection was explained by two factors. First, an important portion of the diet of northern flying squirrels consists of hypogeous fungi (Pyare et al. 2002; Wheatley 2007), which are associated with coarse woody debris (Amaranthus et al. 1994; Carey et al. 1999). Second, the species relies on cavities for nesting and shelter (Wells-Gosling and Heaney 1984; Smith 2007). Recently, however, the flying squirrel was described as a habitat generalist, abundant in mixed or deciduous forests (Wheatley et al. 2005; Holloway and Malcolm 2007) and in even-aged managed or second-growth stands (Rosenberg and Anthony 1992; Ransome and Sullivan 2003). It nests mainly in cavities but also uses external structures built on branches in the forest canopy. External nests can sometimes be located inside witches' brooms, which are deformities of conifer branches caused by dwarf mistletoe (*Arceuthobium* spp.) or spruce rust (*Chrysomyxa* spp.) (Wells-Gosling and Heaney 1984; Smith 2007). There are also

anecdotal accounts of nests in stumps or underground (Gerrow 1996; Bakker and Hastings 2002; Hackett and Pagels 2003).

Much of the geographic range of the northern flying squirrel overlaps with the extent of the boreal biome. As flying squirrels are active all year-round, individuals face extremes of cold weather during the winter, with temperatures as low as -33°C recorded in some studies (Mowrey and Zasada 1984; Cotton and Parker 2000a). Its nocturnal habits, coupled with low mass and a reliance on gliding as a means of locomotion, increase its exposure to cold temperatures. To reduce heat loss and energy expenditure, flying squirrels choose thermally insulated nests (Weigl and Osgood 1974), aggregate in them with many individuals (Mowrey and Zasada 1984; Gerrow 1996), and forage for shorter time periods (Cotton and Parker 2000a). Cavities were proposed as the best winter nest choice (Wells-Gosling and Heaney 1984) because of the superior protection they offer from precipitation, wind, cold temperatures, and predators. However, large cavities adequate for aggregation are scarce in the boreal forest because of short growing seasons and increased industrial logging that limit tree diameters. Suitable cavities could therefore represent a limiting factor to the northern flying squirrel in the boreal forest during winter months.

The objectives of this study were to assess factors affecting site occupancy by northern flying squirrels in the boreal forest to determine whether or not cavities are an important resource, and to identify which nest type is chosen during the colder days of the autumn-winter period. We hypothesized that cavities would represent a limiting factor positively affecting habitat occupancy in the boreal forest because of their limited availability. We also expected that cavities would be more likely to be used than other nest types in cold temperature because of their superior thermal insulation value.

Materials and methods

Site Description

We studied northern flying squirrels in northwestern Quebec at 59 sites, which were located within 50-km of the city of Rouyn-Noranda (48°18'N, 79°05'W), from September 2008 to June 2009. This area is located on the northern Clay Belt and experiences short mild

summers and dry cold winters characteristic of a subarctic climate (mean annual temperature, 1.2°C; precipitation, 914 mm; 158 days with minimum temperature > 0°C; Environment Canada 2009). The study area is in the balsam fir-white birch bioclimatic domain of the boreal forest (Robitaille and Saucier 1998), which consists of mixedwoods of tree species such as trembling aspen (*Populus tremuloides* Michx.), balsam poplar (*Populus balsamifera* L.), white or paper birch (*Betula papyrifera* Marsh.), white spruce (*Picea glauca* (Voss) Moench), black spruce (*Picea mariana* (Mill.) BSP), jack pine (*Pinus banksiana* Lamb.), and balsam fir (*Abies balsamea* (L.) Mill.).

In this region, cavities are mainly created by woodpeckers (P. Drapeau, *personal observation* 2008), and are primarily located (98%) in trembling aspen (Drapeau et al. 2009). This shade-intolerant deciduous species reaches maturity at 60 years and is subsequently prone to fungal rot (Pothier et al. 2004), which renders wood fibres soft and easy to break down by cavity-excavating birds (Jackson and Jackson 2004). We selected even-aged deciduous stands that were dominated by trembling aspen; these stands represented a gradient in stand age (10 to 70 years), and consequently, a gradient in snags and cavity availability. Stand age was determined from 1995 digitized topographic forest maps (1:20,000 scale) produced by the Ministère des Ressources naturelles et de la Faune du Québec (MRNF) using ArcView® 3.2 (ESRI 1999). Other criteria considered for the selection of stands included adjacency to a road that was accessible year-around, a stand area $\geq$ 3.6 ha to ensure a 100-m buffer of homogeneous habitat around the site, and a distance of at least 400 m between sites. The aforementioned values were chosen based on repeated captures of individuals on trapping grids in the Pacific Northwest who moved a mean maximum distance of about 100 meters (Carey 1995). Woodpeckers observed at our sites included the northern flicker (*Colaptes auratus* L.), the yellow-bellied sapsucker (*Sphyrapicus varius* L.), and the downy (*Picoides pubescens* L.), hairy (*P. villosus* L.), and pileated (*Dryocopus pileatus* L.) woodpeckers.

Flying squirrel trapping

We traced an 80-m linear transect that ran perpendicular to the road at each site. We established a trapping station every 10-m along the line transect, for a total of eight stations. We attached a single Tomahawk live trap (Model 201, Tomahawk Live Trap Co., Tomahawk, WI, USA) to the trunk of the closest tree at each trapping station, positioning the

trap horizontally. To test the influence of trap height on capture success (Harestad 1990; Risch and Brady 1996), we established traps at either 1.5- or 4-m above ground level. In any given transect, we randomly assigned the height of the first trap and alternated trap height between 1.5- and 4-m along the eight trapping stations. We reversed height attribution for the second visit (a tree with a trap at 4-m for the first visit received a trap at 1.5-m for the second, and vice-versa). Traps were baited with apple and peanut butter and provided with polyethylene stuffing and white corrugated plastic cover for protection. As flying squirrels are solely active at night, traps were opened at dusk between 16:00 to 21:00, depending on the time of sunset, and checked every morning from 6:00 to 12:00. We trapped 10 sites per week for a period of three consecutive nights until all the sites were visited. We repeated this exercise a second time for a total of two visits over 12 weeks from September to December 2008. We recorded the detection of flying squirrels at each visit for all sites.

Squirrels were anesthetized at first capture with an isoflurane inhaled anesthetic (Desmarchelier et al. 2007), sex was determined, and they were weighed using either a spring- or an electronic-scale. Squirrels were marked with paired, numbered metal ear tags (Monel No.1, National Band & Tag Co., Newport, KY, USA) for individual identification. A sub-group of 46 individuals that weighed > 100 g were fitted with radio collars that weighed 4 g (model PD-2C, Holohil Systems, Ltd., Woodlawn, ON, Canada), and which were attached with plastic cable ties encased in flexible plastic tubing. All manipulations adhered to the Canadian Council on Animal Care Guidelines on the care and use of wildlife and were approved by the institutional animal care review committee at the Université du Québec en Abitibi-Témiscamingue (UQAT).

Nest use

Flying squirrels were radio-tracked while they occupied nests during the day, using a digital receiver (Model R-1000, Communications Specialists, Inc., Orange, CA, USA) and a hand-held three-element Yagi antenna. Radio-tracking was done occasionally in the autumn after the attachment of the collars, and animals were located regularly twice a week from January to April 2009. We used this frequency of sampling as Carey et al (1997) showed that two localizations per week permitted identification of 95% of flying squirrel nests. As flying squirrels never leave their nests during daylight hours (Mowrey and Zasada 1984; Cotton and

Parker 2000a), telemetry tracking was done at any time of day except 30 minutes after dawn or before dusk to ensure that animals were in their nests at the time of radio-tracking. Every time an individual was located, the type of nest being used was recorded, together with characteristics of the tree such as species, diameter at breast height, and status (alive or dead; following Imbeau and Desrochers 2002). Flying squirrels were monitored until death, loss of signal, or removal of collar (from 3 to 203 days). Animals were trapped at their nest locations in spring 2009 to remove collars.

Environmental variables

We measured three habitat variables at each site in May and June 2009 to assess which factor influenced site occupancy by flying squirrels. First, we counted available cavities (cavity availability hypothesis) by conducting a systematic inventory over an area of 1.6 ha using four contiguous transects (200 m long × 20 m wide) perpendicular to the trapping transect. Each of the four transects intersected the trapping transect at a trapping station. All tree trunks were checked for abandoned woodpecker holes (small circular entrances) or natural cavities using binoculars while walking back and forth on the transects, to estimate the total number of cavities per site. All cavity types that are known to be used by the northern flying squirrel were thus counted (Gerrow 1996). Second, we quantified woody debris as a measure of food availability since they provide optimal microhabitat for mushroom growth and because food is also known as a potential limiting factor to northern flying squirrels (food availability hypothesis; Ransome and Sullivan 2004). Using the line intersect sampling method (Marshall et al. 2000) on a 60-m triangular transect crossing the trapping transects at the second and sixth stations, we measured the diameters of all intersecting logs and estimated the volume of woody debris per hectare (m^3/ha). Third, we estimated vegetation cover to assess potential escape from predators (predation avoidance hypothesis). We measured the percentage of lateral cover using the vegetation profile board technique of Nudds (1977) on both sides of the trapping transect at a perpendicular distance of 15 m from the second and fourth stations. We recorded a percentage of obstruction for each of the four 0.5 m sections of the profile board and then, pooled all 16 measurements for each site to obtain a mean percentage.

We assessed the impact of climatic variables on flying squirrel capture success and nest site choice. All data were acquired from the closest meteorological station located in the city of Val-d'Or (48° 03'N, 77°47'W) and downloaded from the Environment Canada website (Environment Canada 2009). For trapping data, we used the minimal temperature from 0:00 to 6:00 over the three night-sampling periods at a site. We also considered total precipitation for these same periods, including the water equivalent of snowfall (i.e., snowfall divided by ten). For telemetry data, we used the minimum temperature from 0:00 to 6:00 on the day of nest localization.

Statistical analysis

We estimated site occupancy rates using the single season model with program PRESENCE 2.4 (Hines 2006; MacKenzie et al. 2006). This method addresses the problem of imperfect detection of animals, common in many species, by estimating a probability of detection using data from repeated visits (MacKenzie et al. 2002). We considered each period of three consecutive nights of trapping at a site as a visit, and each site as independent. We centered all numerical site and environmental variables prior to analysis. We formed sets of candidate models based on the scientific literature to identify the variables that might explain site occupancy by flying squirrels and which affect the probability of detection at each visit. Possible variables influencing site occupancy included habitat measurements: number of cavities (cavity availability hypothesis), lateral cover (predation avoidance hypothesis) and woody debris (food availability hypothesis). We considered temperature, precipitation, trap height, and visit as variables potentially influencing detectability. To quantify the effect of trap height within each site, we split each of the two visits into low or high traps using the design matrix. We ran 10000 bootstrap samples to test the fit of the two global models to the data (where $\hat{c} > 1.0$ indicated overdispersion of the data) and compared candidate models using Akaike's Information Criterion adjusted for small sample size (Burnham and Anderson 2002). We considered models with ΔAICc values ≤ 2 as having strong support and we also calculated model probabilities from the AICc values to indicate the level of support for each model considered (Burnham and Anderson 2002). Following model fitting, we programmed and implemented multimodel inference in R software version 2.9.2 (R Development Core Team 2009) to assess the effect of variables on either occupancy or detection probability.

We compared characteristics of nest trees supporting cavities and trees supporting external nests. First, we used a two-sided t-test on log-transformed values of diameter at breast height (DBH) to assess the difference in means. Second, we used separate chi-square tests to verify that the proportions observed within each category of nest trees were different from a 1:1 ratio for type (deciduous vs. coniferous) and status (alive or dead). Similarly, we assessed the independence of nest type use and sex using a chi-square test. We used mixed logistic regressions separately on each sex to test the influence of temperature and Julian day on the probability of utilization of each of the three nest types (i.e., cavities, external nests, and ground nests). Had observations been independent, a multinomial logistic regression would have been appropriate to model this type of data. Because we had several localizations for each individual, we used a mixed-model counterpart of the multinomial logistic regression instead to reflect the structure of our data (i.e., several observations for each individual). This was achieved by making two comparisons using cavities as the reference level with two logistic regressions and specifying individual as a random effect for each sex. In essence, this is similar to fitting a multinomial logistic regression (see Agresti 2002). The inclusion of animal identity as a random effect in the regressions allowed us to control for possible individual squirrel preferences in nest use. These models were fit with the glmer function of the lme4 package in R (Bates and Maechler 2009).

Results

Environmental variables

We observed considerable variability in all three habitat variables recorded (Fig. 1). Mean number of cavities was 6.9 cavities/site (range 0 - 27), mean volume of woody debris was 64.0 m^3/ha (range 8.4 - 173.7) and mean lateral cover was 57.3% (range 23.6 - 88.8). During autumn trapping, the mean minimum temperature was 0.0°C during the first visit (range -7.4 to 6.4°C) and -9.3°C during the second visit (range -19.1 to 0.3°C). Mean total precipitation for this same period was 6.2 mm for the first visit (range 0 to 16.5 mm) and 7.3 mm for the second visit (range 1.0 to 13.5 mm). During telemetry, minimum temperature averaged -13.6°C (range -40.2 to 7.5°C).

Site occupancy

We surveyed 59 sites twice between 10 September and 5 December 2008 and captured 85 northern flying squirrels (47 males, 38 females) for a total of 102 captures over 2880 trap-nights. The average mass of the animals at the time of capture was similar between sexes and averaged 113.6 ± 2.5 g (S.D. = 10.6) for males and 118.1 ± 2.5 g (S.D. = 14.8) for females. We recorded flying squirrels at least once on 34 sites (58%) with the following detection histories: on both visits at 17 sites (29%), on the first visit only at 14 sites (24%), and on the second visit only at 3 sites (5%). We captured 0-7 flying squirrels per site on each of the two visits, with an average of 1.1 individuals (S.D. = 1.6) on the first visit and 0.6 individuals (S.D. = 1.2) on the second visit.

We considered a total of 18 candidate models for the analysis of site occupancy and detectability, including two global models; the latter were included to avoid collinearity problems between weather variables and visit. Parametric bootstrap did not suggest overdispersion in the data, as the global models had $\hat{c} = 0.9$ and $\hat{c} = 0.8$, respectively. There was considerable uncertainty regarding the most parsimonious model. Indeed, the top-ranked model had an Akaike weight of only 0.17. Seven models were deemed equivalent, having most of the support, including all the variables considered, with Akaike weights ranging from 0.17 to 0.06 (Table 1). The β estimates from model averaging (Table 2) indicate that occupancy is not affected by any of the habitat variables considered in our models. Detection probability decreased with increasing precipitation ($\beta = -0.10$, unconditional SE = 0.03; Fig. 2), was lower using high traps than low traps ($\beta = -0.75$, unconditional SE = 0.35), and was lower during the second visit than during the first visit ($\beta = 0.94$, unconditional SE = 0.34). However, detectability did not vary with temperature. Confidence intervals for model-averaged detectability at 1.5- and 4-m heights overlapped, and this was also the case for detectability between the two visits, because models with the aforementioned variables occurred in models with low Akaike weights (Fig. 3).

Nest use

Collared individuals were radio-tracked between 19 September 2008 and 9 June 2009 to 90 different nests. For nests located within trees, 33 were in cavities (25 woodpecker holes and 8 natural cavities), whereas 34 individuals used external nests, two of which were located

inside a witches' broom. We observed a clear difference in tree use for the above-mentioned nest types (Fig. 4). Cavities were exclusively in deciduous trees (90% trembling aspen), whereas external nests were observed only in conifers ($\chi^2 = 55$, $df = 3$, $P < 0.001$). A greater number of cavities were located in the larger diameter trees that were sampled ($t = 6.8334$, $df = 42$, $P < 0.001$). Cavities were equally frequent in live or dead trees, but external nests exclusively occurred in live trees ($\chi^2 = 23.9761$, $df = 3$, $P < 0.001$). We also located 20 ground nests, four of which were positioned under logs or stumps beneath the snow cover. The remaining ground nests were dug up and appeared to be located below-ground up to depths of 1 m. There were 3 nests located inside the walls of private houses due to the proximity of our sites to residential areas but they were not included in our analysis.

For the logistic regression analyses with random effects, 26 individuals (13 males, 13 females) were located alive in nests a total of 225 times, with 1-34 localizations per animal, from September 2008 to June 2009. Both males and females used cavities, external nests, and ground nests. However, females used a greater proportion of ground nests, while males used mainly external nests ($\chi^2 = 20.3951$, $df = 2$, $P < 0.001$; Fig. 5). We found that the probability of using an external nest compared to a cavity increased significantly with decreasing temperature for males ($\beta = -0.13$, SE = 0.06, $P = 0.048$) but there was no significant effect for females (Table 3, Fig. 6). The probability of using a ground nest rather than a cavity also increased significantly with decreasing temperature for females ($\beta = -0.17$, SE = 0.05, $P < 0.001$), but the low frequency of ground nest use by males prevented analysis. All analyses indicated that Julian day was not an important predictor of nest type use.

Discussion

Site occupancy

We captured northern flying squirrels on more than half our sampled sites (58%) and as many as 7 individuals per site, suggesting high population abundances in aspen-dominated stands of the Abitibi region. We expected that cavity availability would positively affect habitat occupancy in the boreal forest and have stronger support than other habitat variables such as those reflecting food abundance (woody debris) or predation risk (lateral cover). However, none of the habitat variables considered in our analysis explained site occupancy. Although

we could not manipulate the features of habitat, there was sufficient variability across sites to assess the importance of these variables of interest for flying squirrels (Fig. 1). Therefore, we are confident that the observed lack of relationships is not an artifact of a poor range of availability within our sample set.

We found that cavity availability did not influence flying squirrel site occupancy, suggesting they do not represent a limiting factor for this species. Our results corroborate those from nest box supplementation experiments that did not show an increase in population abundance or reproduction rate for either northern flying squirrels in the Pacific Northwest (Carey 2002; Ransome and Sullivan 2004) or southern flying squirrels in South Carolina (Brady et al. 2000). Furthermore, northern flying squirrels are not obligate cavity-nesters in the autumn-winter period, as individuals used other nest types in cold weather during our radio-tracking. Flying squirrels are not territorial and they share and construct nests. This does not support density-dependent relationships required for a resource to limit population size. However, a more robust test of this hypothesis in boreal forests requires experimental manipulation of cavities as well as control of extraneous variables that potentially could confound the results, such as food availability, which has been proposed as the most important factor limiting these populations (Carey et al. 1997; Carey 2002; Ransome and Sullivan 2004).

There were no effects of woody debris or lateral cover on site occupancy. Hypogeous fungi that are consumed by the northern flying squirrel are associated with ground surface woody debris in second-growth and mature stands of the Appalachians and the Pacific Northwest (Amaranthus et al. 1994; Carey et al. 1999; Hackett and Pagels 2003). However, our relatively young stands had a low volume of woody debris with small diameters that was in early stages of decay. Logs in young stands might not represent an adequate substrate for fungal growth, and therefore, they were possibly not an adequate proxy for food availability or an effective predictor of site occupancy for flying squirrels. Similarly, a well-developed understory has been associated with the presence of northern flying squirrel on the west coast of North America (Rosenberg and Anthony 1992; Carey 1995; Pyare and Longland 2002; Smith et al. 2005). In this region, the spotted owl (*Strix occidentalis* Meriam) is a specialized predator of the northern flying squirrel, consuming up to 235 individuals per year, and it typically ambushes prey in open areas (Heinrichs 1983). This owl is absent in eastern Canada

and it is possible that vegetation cover is not as great an influence on predation success or on a flying squirrel's choice of habitat in our study area.

Detection probability was negatively affected by precipitation. Rain with associated cloud cover and low illumination could affect the vision of this nocturnal animal. Precipitation has been shown to negatively influence the ability of northern flying squirrels to orient properly (Flaherty et al. 2008) and to increase latency in moving from release sites during relocation experiments (Rizkalla and Swihart 2007). This behaviour might be coupled with increased thermoregulatory costs and mortality under adverse conditions, as suggested by the observation that Arctic ground squirrel (*Spermophilus parryii* Richardson) stay underground in their burrows on cold rainy days in Alaska (Long et al. 2005). Therefore, flying squirrels might be less active on rainy days, thereby reducing our ability to detect their presence with a trapping method.

Even though model averaging indicated an effect of visit and trap height on detection probabilities, the overlapping confidence intervals in the graphic representation of their predicted values (Fig. 3) indicated poor predictive performance of these two covariates. This is a direct consequence of the models that included these variables of having ranked poorly relative to the entire set of candidate models. The similar success of low (1.5-m) and high traps (4-m) at capturing flying squirrels is contradictory to Risch and Brady (1996), who found that four- to five-m high traps had more southern flying squirrel captures. Our observations of flying squirrels landing on tree trunks and climbing up to the canopy implies that traps would be encountered at any height, especially if the animal is attracted by a strong peanut butter smell. We recommend using low-mounted traps as they do not require the use of a ladder, making them easier to install and monitor.

In this study we could not verify the nest suitability of each hole identified during cavity inventories. A monitoring study of cavities in Abitibi using telescopic cameras has found a strong relationship between hole density (holes with uncompleted cavities) and "true" cavity density, with a constant proportion (40%) of holes representing suitable cavities across habitat and forest stand age (Ouellet-Lapointe, U., Imbeau L., Drapeau, P. and Cadieux, P., *in review*). Therefore, we assumed a similar error across our sites for relative cavity availability

and we are thus conservative in our estimates of cavity availability without, however, affecting the range of cavity availability in our sample set. We could not differentiate between age classes of flying squirrels during trapping and we included all captured individuals in our analysis. Physical characteristics used to distinguish juveniles from adults (Villa et al. 1999) could not be identified successfully during our manipulations. However, Ransome and Sullivan (2004) assumed that no adult flying squirrels were less than 100 g. Only 6 individuals were under this limit in our sample, and of this group, two were the only animals captured at a given site. We believe that juveniles dispersing during the autumn did not bias our site occupancy results as they did not represent a large proportion of individuals captured.

Nest use

We located 26 live animals to their nests during autumn and winter 2008-2009, and identified the nest type as a cavity, an external nest, or a ground nest. We expected cavities to be chosen in cold temperatures because of their superior thermal insulation properties. However, analysis of telemetry localizations shows that, even if cavities are used by northern flying squirrels in the boreal forest during the autumn-winter period, they are not chosen when the temperature decreased.

External nests had the highest proportion of use, with 39% of all localizations, and were more likely to be used than cavities in cold weather by males. This result is similar to that of a study in interior Alaska, which reported a majority of nest locations (65%) in outside nests and an avoidance of cavities in conditions of extreme cold (Mowrey and Zasada 1984). However, most northern studies have reported low use of external nests in favor of cavities (4% in Alberta, McDonald 1995; 16% in northwestern British Columbia, Cotton and Parker 2000b; $\leq$ 27% in southeastern Alaska, Bakker and Hastings 2002; 29% in central Ontario, Holloway and Malcolm 2007). In New Brunswick, external nests represented 40% of all nests found; however, they were avoided during winter (Gerrow 1996). This avoidance was explained by the wet, cold climate of the coast and the tendency of external nests to freeze after water absorption, limiting insulation qualities. The construction of external nests by the northern flying squirrel does offer numerous advantages during the cold season. First, external nests can be located in structures that provide additional protection. As in other

studies, we observed external nests mainly in the dense foliage of live coniferous trees of small diameter (Weigl et al. 1992; Carey et al. 1997; Holloway and Malcolm 2007). Second, they can be located close to food sources, further reducing travel costs, energetic demands, and predation risks. Third, their adaptable size increases the potential for aggregations. Aggregations have been correlated with drops in temperatures (Mowrey and Zasada 1984; Gerrow 1996; Cotton and Parker 2000a) and have been shown to reduce energy expenditures up to 33% in southern flying squirrels (Stapp et al. 1991). In Abitibi, it is possible that external nests provide the northern flying squirrel with high insulation cover because of the dry climate, the choice of a strategic location, and the possibility to form aggregations.

We found that ground nests were the second-most used nests, with 35% of all localizations, and that they were more likely to be used than cavities by females in cold temperatures. This is surprising as only a few studies have observed the use of ground or subterranean nests by northern flying squirrels (9.8% in southern New Brunswick, Gerrow 1996; 8% in southeastern Alaska, Bakker and Hastings 2002; 27% for males in southwest Virginia, Hackett and Pagels 2003; 0.02% in central Ontario, Holloway and Malcolm 2007). Gerrow (1996) also found an increased use of ground nests with decreasing temperature in winter. It is very possible that the insulation provided by a ground nest is superior to any other nest type because of the insulative properties of snow and that the use of ground nests may represent normal winter behaviour in a cold climate. There might also be a compromise between insulation and predation, as we observed eight mortalities in underground nests over the course of the study. Gerrow (1996) suggested weasels were the only predators capable of getting into underground nests and observed that weasel predation upon flying squirrels increased with the latter's increased use of ground nests. In Alaska, the relatively frequent use of below-ground nests suggests that thermoregulatory gain can outweigh the added predation risk of denning near ground-level (Bakker and Hastings 2002).

Nest choice was clearly differentiated by sex, with males using external nests and females using ground nests. Females have been observed to use low structures such as stumps and slash piles as natal dens during the reproductive period in the Pacific Northwest (Carey et al. 1997) and it is known that females isolate themselves to raise their young (Gerrow 1996). Carey et al. (1997) hypothesized that only suboptimal nests are available when the number of

cavities is low and competition is high. We made all our observations of ground nest use outside the breeding season (parturition: late May through June, Wells-Gosling and Heaney 1984), suggesting a thermoregulatory basis to the use of ground nests. Further, we believe the difference in nest use by sex might have been due to sample size, as most collared males did not survive through the winter. In fact, 76% of male localizations in temperatures < 0°C (n = 63) were made on three males, and one of these did not use ground nests at all. Spatial and temporal use of nests varies among individuals (Cotton and Parker 2000b; Hackett and Pagels 2003). There might have been an individual preference towards external nests in the cold, and thus, our small sample size shows low use of ground nests by males.

It is possible that cavities do not provide sufficient insulation for the cold winter period in the boreal forest. Cavities are used by both males (24%) and females (27%), but they are less likely to be used as temperature decreases. In New Brunswick, the use of excavated cavities decreased with decreasing temperature in winter (Gerrow 1996). Wiebe (2001) has demonstrated that cavities in live and large trembling aspen heat and cool more slowly than small and dead trees, resulting in more stable temperatures during the day. This response is partly because large trees have thick walls surrounding the cavity, thereby providing better insulation. This temperature moderating effect is illustrated by cavities being 6.5°C warmer than nest boxes (McComb and Noble 1981). Interestingly, the only two cavities used below -15°C were in large trees of 49- and 34-cm DBH, which were among the four largest cavity trees used for nesting by northern flying squirrels during our study. Although cavities were largely used (96%) during the autumn-winter period in Alberta, trees had an average diameter of 36.5 cm and live trees were used (McDonald 1995). This suggests they were better insulated than in our sites. Therefore, cavities in large trees are probably limited in our study area and small trees might not offer adequate thermal insulation for winter.

We found that northern flying squirrels were opportunistic in their nest use. Cavities used by flying squirrels were located mostly in large trembling aspen, either dead or live individuals, reflecting the selection by woodpeckers for this deciduous species, which is commonly infected by heartwood rot (Wiebe 2001; Savignac and Machtans 2006). Similarly, heartwood decay and tree size were important in determining nest-trees for northern flying squirrels in central Ontario and these characteristics were determined by the excavators (Holloway and

Malcolm 2007). Flying squirrels have also been observed to use nest types or nest trees reflecting what is available in the area (McDonald 1995; Gerrow 1996). We did not observe the choice of one specific nest type; rather, our results support other studies that have shown the flying squirrel can use a variety of structures and is highly flexible. It is opportunistic in its choice of structures to be used, even though it generally seeks larger trees (McDonald 1995; Gerrow 1996; Cotton and Parker 2000b; Hackett and Pagels 2003).

In conclusion, the hypothesis that cavities represent a limiting factor during winter months in the boreal forest was not supported. The northern flying squirrel was present and abundant in our aspen-dominated stands in Abitibi. However, site occupancy was not influenced by cavity availability and cavities were not chosen when air temperature dropped. We recognize that flying squirrels use cavities, but these resources are not essential during the cold seasons of autumn-winter. This species could thus be considered a generalist, able to use a variety of different nest structures. This would explain the abundance and broad distribution of the species across a wide range of environments and its distributional range reaching high northern latitudes.

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References

Aitken, K.E.H., Wiebe, K.L., and Martin, K. 2002. Nest-site reuse patterns for a cavity-nesting bird community in interior British Columbia. Auk **119**(2): 391-402. doi:10.1642/0004-8038(2002)119[0391:nsrpfa]2.0.co;2.

Agresti, A. 2002. Categorical data analysis. John Wiley & Sons, Inc., Hoboken, NJ.

Amaranthus, M., Trappe, J.M., Bednar, L., and Arthur, D. 1994. Hypogeous fungal production in mature Douglas-Fir forest fragments and surroundings plantations and its relation to coarse woody debris and animal mycophagy. Can. J. For. Res. **24**(11): 2157-2165. doi:10.1139/x94-278.

Blanc, L.A. and J.R. Walters. 2008. Cavity excavation and enlargement as mechanisms for indirect interactions in an avian community. Ecology **89**(2): 506-514. doi: 10.1890/07-0219.1

Bakker, V.J., and Hastings, K. 2002. Den trees used by northern flying squirrels (*Glaucomys sabrinus*) in southeastern Alaska. Can. J. Zool. **80**(9): 1623-1633. doi:10.1139/z02-155

Bates, D. and Maechler, M. 2009. lme4: Linear mixed-effects models using S4 classes [online]. R package version 0.999375-31. Available from CRAN.R-project.org/package=lme4 [accessed 5 September 2009].

Brady, M.J., Risch, T.S., and Dobson, F.S. 2000. Availability of nest sites does not limit population size of southern flying squirrels. Can. J. Zool. **78**(7): 1144-1149. doi:10.1139/cjz-78-7-1144

Burnham, K.P., and Anderson, D.R. 2002. Model selection and multimodel inference: a practical information-theoretic approach. 2nd ed. Springer-Verlag, New York, NY.

Carey, A.B. 1995. Sciurids in Pacific Northwest managed and old-growth forests. Ecol. Appl. **5**(3): 648-661. doi:10.2307/1941974

Carey, A.B. 2002. Response of northern flying squirrels to supplementary dens. Wildl. Soc. Bull. **30**(2): 547-556.

Carey, A.B., Wilson, T.M., Maguire, C.C., and Biswell, B.L. 1997. Dens of northern flying squirrels in the Pacific Northwest. J. Wildl. Manage. **61**(3): 684-699.

Carey, A.B., Kershner, J., Biswell, B., and de Toledo, L.D. 1999. Ecological scale and forest development: Squirrels, dietary fungi, and vascular plants in managed and unmanaged forests. Wildl. Monogr. **142**(1): 5-71.

Cotton, C.L., and Parker, K.L. 2000a. Winter activity patterns of northern flying squirrels in sub-boreal forests. Can. J. Zool. **78**(11): 1896-1901. doi:10.1139/cjz-78-11-1896

Cotton, C.L., and Parker, K.L. 2000b. Winter habitat and nest trees used by northern flying squirrels in subboreal forests. J. Mammal. **81**(4): 1071-1086. doi:10.1644/1545-1542(2000)081<1071:whantu>2.0.co;2.

Desmarchelier, M., Cheveau, M., Imbeau, L., and Lair, S. 2007. Field use of isoflurane as an inhalant anesthetic in the American marten (*Martes americana*). J. Wildl. Dis. **43**(4): 719-725.

Drapeau, P., Nappi, A., Imbeau, L., and Saint-Germain, M. 2009. Standing deadwood for keystone bird species in the eastern boreal forest: Managing for snag dynamics. Forestry Chron. **85**(2): 227-234.

Environment Canada. 2009. Canadian Climate Normals 1971-2000 [online]. Available from climate.weatheroffice.ec.gc.ca [accessed 14 December 2009].

ESRI. 1999. ArcView® GIS. Environmental Systems Research Institute, Inc., Redlands, CA.

Flaherty, E.A., Smith, W.P., Pyare, S., and Ben-David, M. 2008. Experimental trials of the northern flying squirrel (*Glaucomys sabrinus*) traversing managed rainforest landscapes: perceptual range and fine-scale movements. Can. J. Zool. **86**(9): 1050-1058. doi:10.1139/ z08-084.

Gerrow, J.S. 1996. Home range, habitat use, nesting ecology and diet of the northern flying squirrel in southern New Brunswick. M.Sc. thesis, Acadia University, Wolfville, NS.

Hackett, H.M., and Pagels, J.F. 2003. Nest site characteristics of the endangered northern flying squirrel (*Glaucomys sabrinus coloratus*) in southwest Virginia. Am. Midl. Nat. **150**(2): 321-331.

Harestad, A.S. 1990. Nest site selection by northern flying squirrels and Douglas squirrels. Northwest Sci. **71**: 43-45.

Harrison, H.H. 1975. A field guide to birds' nests of 285 species found breeding in the United States east of the Mississippi River. Houghton Mifflin Company, Boston, MA.

Heinrichs, J. 1983. The winged snail darter. J. Forest. **81**: 212-215, 262.

Hines, J.E. 2006. PRESENCE2- Software to estimate patch occupancy and related parameters [online]. Available from mbr-pwrc.usgs.gov/software/presence.html [accessed 5 October 2009].

Holloway, G.L., and Malcolm, J.R. 2007. Nest-tree use by northern and southern flying squirrels in central Ontario. J. Mammal. **88**(1): 226-233.

Imbeau, L., and Desrochers, A. 2002. Foraging ecology and use of drumming trees by three-toed woodpeckers. J. Wildl. Manage. **66**(1): 222-231.

Jackson, J.A., and Jackson, B.J.S. 2004. Ecological relationships between fungi and woodpecker cavity sites. Condor **106**(1): 37-49.

Long, R.A., Martin, T.J., and Barnes, B.M. 2005. Body temperature and activity patterns in free-living Arctic ground squirrels. J. Mammal. **86**(2): 314-322. doi:10.1644/brg-224.1.

MacKenzie, D.I., Nichols, J.D., Lachman, G.B., Droege, S., Royle, J.A., and Langtimm, C.A. 2002. Estimating site occupancy rates when detection probabilities are less than one. Ecology **83**(8): 2248-2255. doi:10.1890/0012-9658(2002)083[2248:esorwd]2.0.co;2

MacKenzie, D.I., Nichols, J.D., Royle, J.A., Pollock, K.H., Bailey, L.L., and Hines, J.E. 2006. Occupancy estimation and modeling - inferring patterns and dynamics of species occurence. Academic Press, New York, NY.

Marshall, P.L., Davis, G., and LeMay, V.M. 2000. Using line intercept sampling for coarse woody debris. Technical Report TR-003, Vancouver Forest Region Research Section, BC Ministry of Forests, Nanaimo, BC.

Martin, K., and Eadie, J.M. 1999. Nest webs: A community-wide approach to the management and conservation of cavity-nesting forest birds. For. Ecol. Manag. **115**(2-3): 243-257. doi:10.1016/s0378-1127(98)00403-4

Martin, K., K.E.H. Aitken and K.L. Wiebe. 2004. Nest sites and nest webs for cavity-nesting communities in Interior British Columbia, Canada: Nest characteristics and niche partitioning. Condor **106**(1): 5–19. doi: 10.1668/1540-7063.

McComb, W.C., and Noble, R.E. 1981. Microclimate of nest boxes and natural cavities in bottomland hardwoods. J. Wildl. Manage. **45**(1): 284-289.

McDonald, L. 1995. Relationships between northern flying squirrels and stand age and structure in aspen mixedwood forests in Alberta. *In* Relationships between stand age, stand structure, and biodiversity in aspen mixedwood forests in Alberta. *Edited by* J.B. Stelfox. Jointly published by Alberta Environmental Centre (AECV95-R1), Vegreville, AB, and Canadian Forest Service (Project No. 0001A), Edmonton, AB. pp. 227-240.

Mowrey, R.A., and Zasada, J.C. 1984. Den tree use and movements of northern flying squirrels in interior Alaska and implications for forest management. *In* Fish and wildlife relationships in old-growth forests: proceedings of a symposium, Juneau, Alaska, 12-15 April, 1982. *Edited by* W.R. Mechan, T.R. Merrell Jr., and T.A. Hanley. American Institute of Fishery Research Biologists, Juneau, Alaska. pp. 351-356.

Newton, I. 1994. The role of nest sites in limiting the numbers of hole-nesting birds: A review. Biol. Conserv. **70**(3): 265-276. doi:10.1016/0006-3207(94)90172-4.

Nudds, T.D. 1977. Quantifying the vegetative structure of wildlife cover. Wildl. Soc. Bull. **5**(3): 113-117.

Pothier, D., Raulier, F., and Riopel, M. 2004. Ageing and decline of trembling aspen stands in Quebec. Can. J. For. Res. **34**(6): 1251-1258. doi:10.1139/x04-017

Pyare, S., and Longland, W.S. 2002. Interrelationships among northern flying squirrels, truffles, and microhabitat structure in Sierra Nevada old-growth habitat. Can. J. For. Res. **32**(6): 1016-1024. doi:10.1139/x02-002.

Pyare, S., Smith, W.P., Nicholls, J.V., and Cook, J.A. 2002. Diets of northern flying squirrels, *Glaucomys sabrinus*, in southeast Alaska. Can. Field-Nat. **116**(1): 98-103.

R Development Core Team. 2009. R: A language and environment for statistical computing [online]. R Foundation for Statistical Computing, Vienna, Austria. ISBN 3-900051-07-0, Available from www.R-project.org [accessed 5 September 2009].

Ransome, D.B., and Sullivan, T.P. 2003. Population dynamics of *Glaucomys sabrinus* and *Tamiasciurus douglasii* in old-growth and second-growth stands of coastal coniferous forest. Can. J. For. Res. **33**(4): 587-596. doi:10.1139/x02-193

Ransome, D.B., and Sullivan, T.P. 2004. Effects of food and den-site supplementation on populations of *Glaucomys sabrinus* and *Tamiasciurus douglasii*. J. Mammal. **85**(2): 206-215. doi:10.1644/bos-118.

Risch, T.S., and Brady, M.J. 1996. Trap height and capture success of arboreal small mammals: Evidence from southern flying squirrels (*Glaucomys volans*). Am. Midl. Nat. **136**(2): 346-351.

Rizkalla, C.E., and Swihart, R.K. 2007. Explaining movement decisions of forest rodents in fragmented landscapes. Biol. Conserv. **140**(3-4): 339-348. doi:10.1016/j.biocon.2007.08.019.

Robitaille, A., and Saucier, J.-P. 1998. Paysages régionaux du Québec méridional. Les publications du Québec, Sainte-Foy, QC.

Rosenberg, D.K., and Anthony, R.G. 1992. Characteristics of northern flying squirrel populations in young second-growth and old-growth forests in western Oregon. Can. J. Zool. **70**(1): 161-166. doi:10.1139/z92-023

Savignac, C., and Machtans, C.S. 2006. Habitat requirements of the Yellow-bellied Sapsucker, *Sphyrapicus varius*, in boreal mixedwood forests of northwestern Canada. Can. J. Zool. **84**(9): 1230-1239. doi:10.1139/z06-112.

Sedgwick, J.A., and Knopf, F.L. 1992. Cavity turnover and equilibrium cavity densities in a cottonwood bottomland. J. Wildl. Manage. **56**(3): 477-484.

Smith, W.P. 2007. Ecology of *Glaucomys Sabrinus*: Habitat, demography, and community relations. J. Mammal. **88**(4): 862-881. doi:10.1644/06-mamm-s-371r1.1.

Smith, W.P., Gende, S.M., and Nichols, J.V. 2005. The northern flying squirrel as an indicator species of temperate rain forest: Test of an hypothesis. Ecol. Appl. **15**(2): 689-700. doi:10.1890/03-5035

Stapp, P., Pekins, P.J., and Mautz, W.W. 1991. Winter energy expenditure and the distribution of southern flying squirrels. Can. J. Zool. **69**(10): 2548-2555. doi:10.1139/z91-359

Villa, L.J., Carey, A.B., Wilson, T.M., and Glos, K.E. 1999. Maturation and reproduction of northern flying squirrels in Pacific Northwest forests. Gen. Tech. Rep. PNW-GTR-444, Pacific Northwest Research Station, United States Department of Agriculture, Portland, OR.

Weigl, P.D., Knowles, T.W., and Boynton, A.C. 1992. The distribution and ecology of the northern flying squirrel, *Glaucomys sabrinus coloratus*, in the southern Appalachians. Nongame and Endangered Wildlife Program, North Carolina Wildlife Resources Commission, Raleigh, NC.

Weigl, P.D., and Osgood, D.W. 1974. Study of the northern flying squirrel, *Glaucomys sabrinus*, by temperature telemetry. Am. Midl. Nat. **92**(2): 482-486.

Wells-Gosling, N., and Heaney, R.N. 1984. *Glaucomys sabrinus*. Mamm. Species No. **229**: 1-8.

Wheatley, M. 2007. Fungi in summer diets of northern flying squirrels (*Glaucomys sabrinus*) within managed forests of western Alberta, Canada. Northwest Sci. **81**(4): 265-273. doi:10.3955/0029-344x-81.4.265.

Wheatley, M., Fisher, J.T., Larsen, K., Litke, J., and Boutin, S. 2005. Using GIS to relate small mammal abundance and landscape structure at multiple spatial extents: the

northern flying squirrel in Alberta, Canada. J. Appl. Ecol. **42**(3): 577-586. doi:10.1111/j.1365-2664.2005. 01034.x.

Wiebe, K.L. 2001. Microclimate of tree cavity nests: Is it important for reproductive success in northern flickers? Auk **118**(2): 412-421. doi:10.1642/0004-8038(2001)118[0412:motcni] 2.0.co;2.

Table 1. Model selection results for northern flying squirrel occupancy (ψ) and detection probability (*p*) in Abitibi, Québec, Canada, during autumn 2008.

Models	K[a]	AIC_c[b]	ΔAIC_c[c]	w_i[d]	Deviance[e]
ψ(Cav), *p*(Ppt)	4	259.84	0.00	0.17	251.10
ψ(LC), *p*(Ppt)	4	260.01	0.17	0.16	251.27
ψ(LC), *p*(v)	4	260.66	0.82	0.11	251.92
ψ(WD), *p*(Ppt)	4	260.72	0.88	0.11	251.97
ψ(Cav), *p*(v)	4	260.79	0.95	0.11	252.05
ψ(Cav+LC+WD), *p*(Ht+Temp+Ppt)	8	261.13	1.29	0.09	242.25
ψ(WD), *p*(v)	4	261.83	1.99	0.06	253.09
ψ(Cav+LC+WD), *p*(Ht+v)	7	262.01	2.17	0.06	245.81
ψ(LC), *p*(Ht)	4	263.95	4.11	0.02	255.21
ψ(Cav), *p*(Ht)	4	264.08	4.24	0.02	255.34
ψ(LC), *p*(Temp)	4	264.56	4.72	0.02	255.82
ψ(Cav), *p*(Temp)	4	264.84	5.00	0.01	256.09
ψ(WD), *p*(Ht)	4	265.11	5.27	0.01	256.37
ψ(.), *p*(.)	2	265.21	5.37	0.01	261.00
ψ(WD), *p*(Temp)	4	265.89	6.05	0.01	257.15
ψ(LC), *p*(.)	3	266.20	6.36	0.01	259.76
ψ(Cav), *p*(.)	3	266.35	6.51	0.01	259.91
ψ(WD), *p*(.)	3	267.36	7.52	0.00	260.92

[a]K = no. of parameters.

[b]AIC_c = Akaike's Information Criterion corrected for small sample sizes.

[c]ΔAIC_c = AIC_c relative to the most parsimonious model.

[d]w_i = AIC_c model weight.

[e]deviance = -2×log-likelihood.

Table 2. Model-averaged parameter estimates (β_i) on the logit scale for northern flying squirrel detection probability and site occupancy models in Abitibi, Québec, Canada, during autumn 2008. Reference levels are shown in parentheses for qualitative covariates. The values in boldface print identify variables for which confidence interval did not include zero.

Parameter	Estimate	Unconditional SE	Lower 95% CL	Upper 95% CL
Occupancy				
Cavity availability	-0.07	0.06	-0.19	0.06
Lateral cover	0.02	0.02	-0.03	0.07
Woody debris	0.00	0.01	-0.02	0.02
Detection				
Height (low)	-0.75	0.35	**-1.43**	**-0.07**
Precipitation	-0.10	0.03	**-0.16**	**-0.03**
Temperature	0.04	0.02	0.00	0.09
Visit (2)	0.94	0.34	**0.27**	**1.62**

Table 3. Result of logistic regression with random effects for individuals conducted on nest type use by northern flying squirrels in Abitibi, Québec, Canada, during autumn-winter 2008-2009. Note that a multinomial logistic regression approach was used by conducting two analyses for each sex sensu Agresti (2002). The first model used probability of choosing an external nest vs. cavity as a response variable, and the second model used probability of choosing a ground nest vs. cavity as a response variable.

Comparison	Parameter	Estimate	SE	z value	*P*
External nest					
	Female				
	Intercept	0.29	1.41	0.21	0.84
	Temperature	-0.09	0.06	-1.52	0.13
	Julian Day	-0.01	0.01	-0.76	0.45
	Male				
	Intercept	-2.19	1.22	-1.79	0.07
	Temperature	-0.13	0.06	-1.98	0.05
	Julian Day	0.02	0.01	1.69	0.09
Ground nest					
	Female				
	Intercept	-1.38	1.87	-0.74	0.46
	Temperature	-0.17	0.05	-3.65	<0.001
	Julian Day	-0.02	0.01	-1.67	0.09
	Male				
	DATA TOO SPARSE				

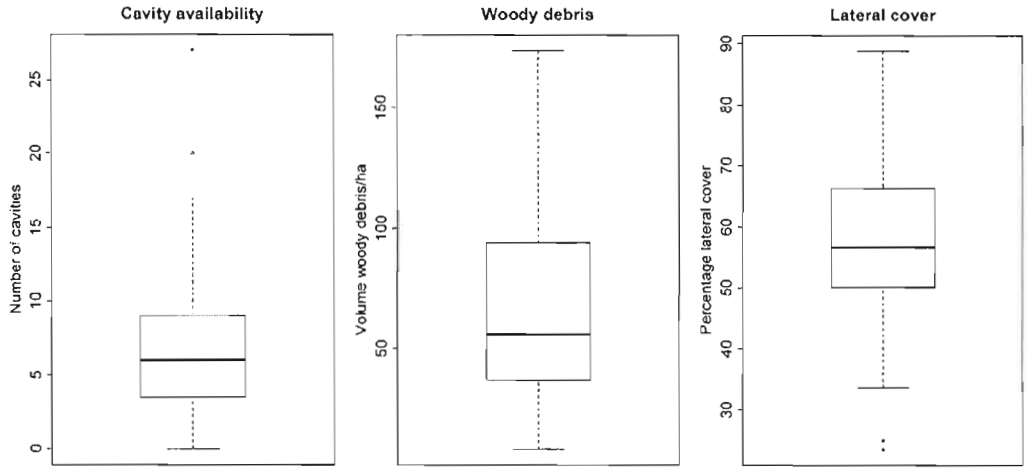

Figure 1. Box and whisker plots showing variability in the three habitat variables measured at each of 59 sites in Abitibi, Québec, during spring 2009. The bold line is the 50th percentile (median), lower edge of box is the 25th percentile, upper edge of box is 75th percentile, while the whiskers represent the lower 10th and 90th percentiles of the data. Points are outliers.

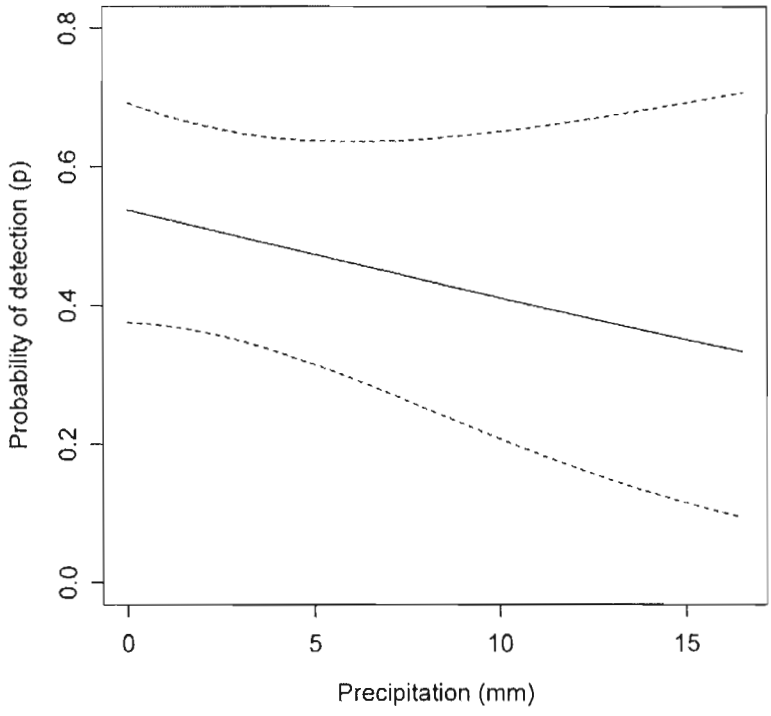

Figure 2. Effect of precipitation on detection probability of northern flying squirrels in Abitibi, Québec, Canada, during autumn 2008. Results based on the model-averaged predictions. We used low-mounted traps and first visits for the qualitative covariates and set temperature to its mean value across visits. Dashed lines indicate 95% confidence intervals.

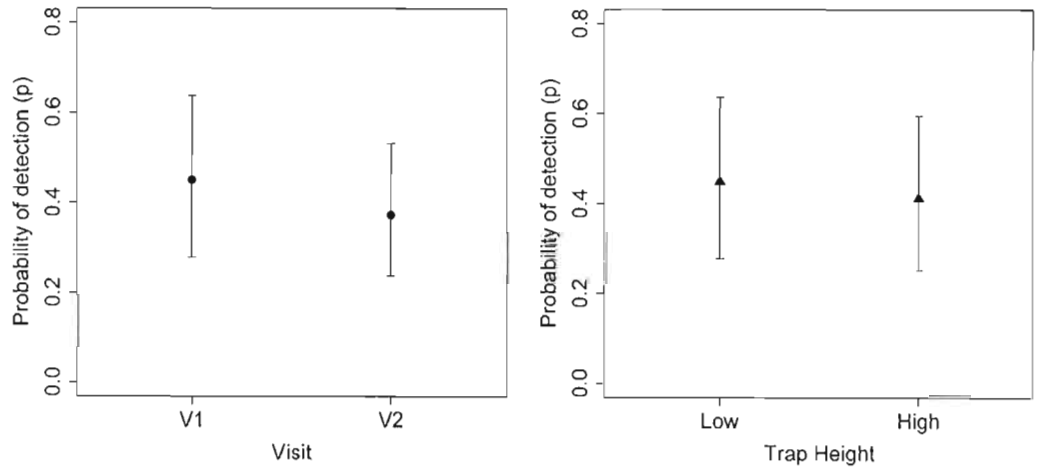

Figure 3. Effect of visit and trap height on the detection probability of northern flying squirrels in Abitibi, Québec, Canada, during autumn 2008. Results are based on model-averaged predictions. We used low-mounted traps and first visits for the qualitative covariates and set temperature and precipitation to their mean values across visits. Error bars indicate 95% confidence intervals.

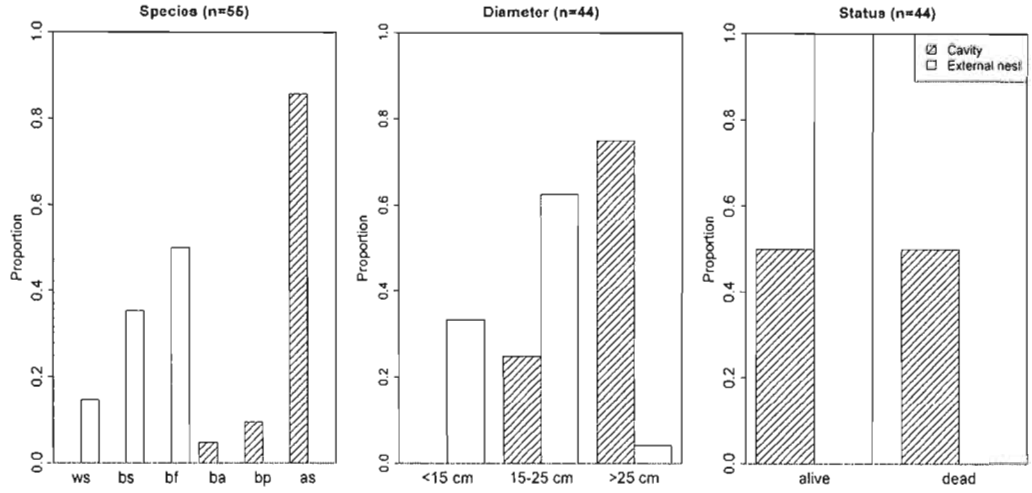

Figure 4. Comparison of species, diameter, and status of trees used by northern flying squirrels as diurnal refuge in Abitibi, Québec, during the autumn-winter period of 2008-2009. Species abbreviations: ws = white spruce, bs = black spruce, bf = balsam fir, ba = black ash, bp = balsam poplar, and as = trembling aspen.

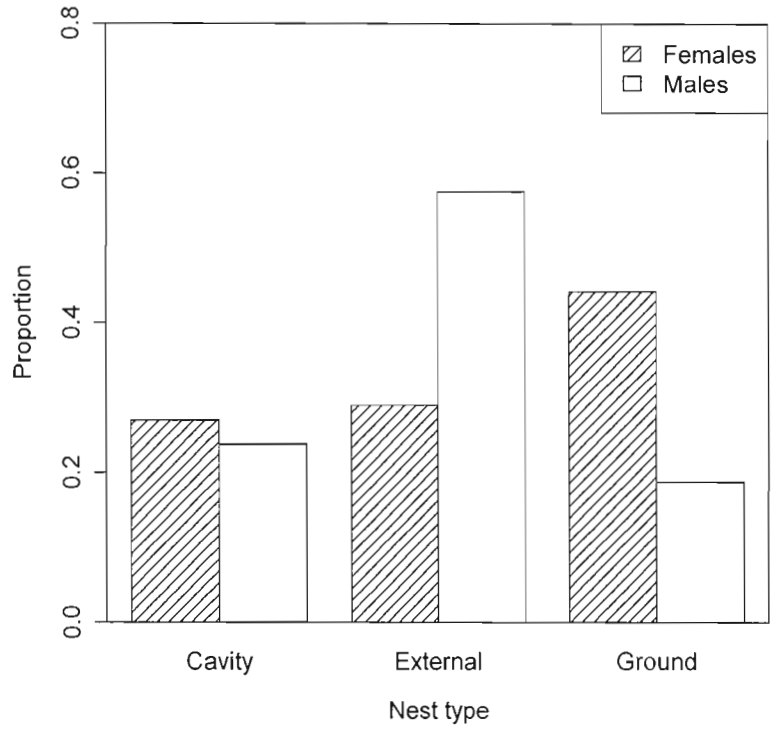

Figure 5. Proportion of localizations in each nest type by sex: female (n = 145) and male (n = 80) northern flying squirrels in Abitibi, Québec, Canada, during the autumn-winter period of 2008-2009.

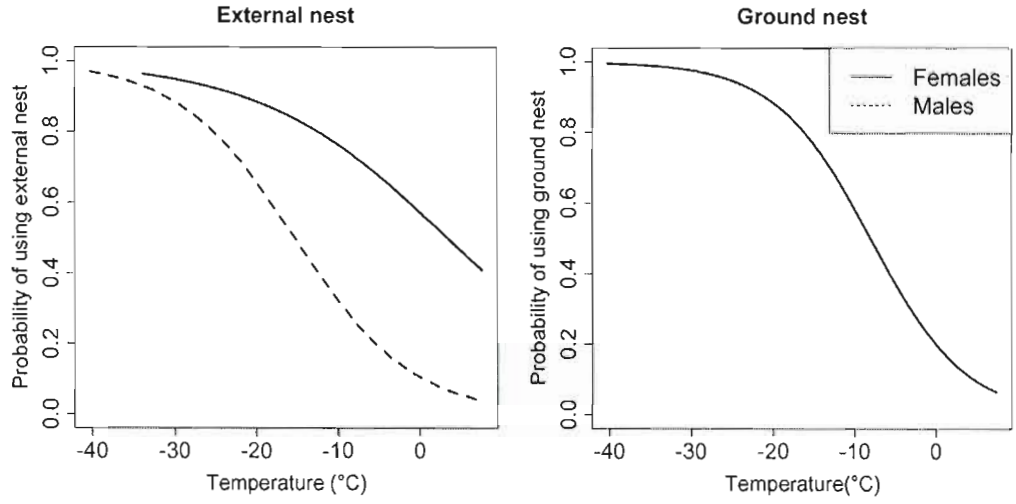

Figure 6. Effect of temperature on the probability of using an external and a ground nest by females and males northern flying squirrel in Abitibi, Québec, Canada during autumn-winter 2008-2009. Reference level for comparisons is cavity. Limited use of ground nests by males prevented analysis.

CONCLUSION GÉNÉRALE

Cette étude avait pour objectif de déterminer la sélection d'habitat et l'importance des cavités en période hivernale pour le Grand Polatouche dans la forêt boréale mixte. Elle a été réalisée dans une région où la disponibilité de cavité est naturellement faible, et pendant les saisons froides de l'automne et l'hiver qui représentent une contrainte énergétique pour les petits mammifères, tel le Grand Polatouche. Dans ces conditions, les cavités pouvaient offrir un avantage au niveau de la conservation d'énergie puisqu'elles sont reconnues pour offrir un isolant thermique supérieur aux autres types de nid. Ainsi, les cavités avaient le potentiel de représenter un facteur limitant pour les populations de Grand Polatouche. L'étude répondait aussi à un besoin d'acquisition de connaissances puisque la sélection d'habitat de cette espèce est très peu connue en forêt boréale, particulièrement dans l'est du Canada.

Les résultats du premier chapitre montrent que la proportion de forêt résineuse dans une zone tampon correspondant à la distance de dispersion médiane du Grand Polatouche (430 m) influence négativement la présence de l'espèce à un site de nichoirs. Ces résultats supportent l'hypothèse que le Grand Polatouche n'est pas un spécialiste des forêts de conifères comme il est stipulé dans la littérature scientifique pour d'autres régions. Les forêts de feuillus représentent un habitat d'intérêt pour le Grand Polatouche en forêt boréale mixte, possiblement dû à une plus grande proportion de Peuplier faux-tremble et donc une plus grande disponibilité de cavités. Par contre, les hypothèses ont été rejetées en ce qui a trait à l'effet de la proportion de forêts matures ou âgées et des habitats ouverts sur la présence de l'espèce aux sites. En effet, ces variables n'ont eu aucun effet sur l'occupation hivernale des sites étudiés. Il semble que dans l'étendue de conditions environnementales rencontrées dans notre aire d'étude, le Grand Polatouche soit capable d'utiliser une variété d'habitats et il n'est contraint ni d'habiter uniquement les forêts matures ou vieilles ni d'éviter les sites à proximité de milieux ouverts qui limitent le vol plané. Pour ce qui est de la détection de l'espèce aux nichoirs, elle s'est avérée être positivement influencée par la température. L'hypothèse était plutôt que le Grand Polatouche allait utiliser les nichoirs préférablement en période froide puisque ces derniers protègent des intempéries de façon similaire aux cavités. Il est possible que l'agrégation de plusieurs individus dans les nids lors des nuits plus froides

ait limité la probabilité de détection dans de telles conditions. Par contre, le deuxième chapitre de cette étude suggère que l'espèce préfère utiliser d'autres types de nid en période froide.

Les résultats du deuxième chapitre corroborent les conclusions du chapitre précédent quant à l'utilisation des forêts de feuillus par le Grand Polatouche. En effet, l'espèce a été capturée dans plus de la moitié des sites de piégeage à dominance de Peuplier faux-tremble et en relative forte abondance. Contrairement à nos prévisions, les cavités ne semblent pas représenter un facteur limitant pour le Grand Polatouche pendant la période hivernale. En effet, dans notre aire d'étude, la disponibilité de cavités n'influençait pas la probabilité d'occupation des sites par cette espèce. Une conclusion similaire a été obtenue pour les indices de disponibilité de nourriture (débris ligneux grossiers) ou de protection contre la prédation (couvert latéral). De plus, le suivi télémétrique d'une quarantaine d'individus a permis de démontrer que les cavités sont utilisées pendant l'automne et l'hiver, mais que le Grand Polatouche ne les préfère pas lorsque les températures diminuent. Les mâles préfèrent plutôt utiliser les nids externes construits dans la canopée, alors que les femelles utilisent les nids souterrains ou situés sous la neige. Ce choix pourrait être lié à la valeur isolante de chaque type de nid ou à la capacité d'y contenir plusieurs individus. Encore une fois, le Grand Polatouche utilise des habitats avec des caractéristiques variées ainsi que différents types de nids. Le Grand Polatouche est donc généraliste dans son utilisation de l'habitat à diverses échelles. Ceci pourrait expliquer sa large distribution géographique à travers l'Amérique du Nord jusqu'à une latitude qui correspond à la limite de la forêt.

Comme la majorité des études réalisées en milieu naturel et non contrôlé, ce projet comporte certaines limites et points faibles. D'abord, en raison de contraintes monétaires et logistiques, l'étude n'a pu être réalisée que sur une seule année. Plusieurs facteurs variant annuellement peuvent influencer les populations de petits mammifères, tels que l'abondance de nourriture ou de prédateurs et les conditions météorologiques. Ainsi, une étude similaire conduite sur plusieurs années dans la même région permettrait de confirmer les résultats obtenus. Aussi, ce projet ciblait la période hivernale à titre de période critique pour cette espèce au niveau de l'utilisation de l'habitat. Par contre, les résultats ont montré une sélection de nids différente pour les mâles et les femelles en hiver et une utilisation plus importante des nichoirs en

réponse à l'augmentation de la température au printemps. Sachant que les femelles sélectionnent les cavités en période de mise bas dans d'autres études, ceci suggère un effet potentiel de la période de reproduction sur l'utilisation des cavités en forêt boréale mixte. Il est donc impossible de conclure sur l'importance des cavités pour cette espèce sans avoir étudié l'utilisation de nids à cette période de l'année. Finalement, il faut reconnaître que les données des cartes écoforestières ne sont pas parfaitement à jour dû au délai nécessaire à leur production, particulièrement dans le cas des lots forestiers privés. Elles représentent donc un biais inhérent à l'étude. Par contre, elles offrent tout de même une représentation fidèle du paysage et, à défaut de meilleures données, permettent tout de même l'acquisition de connaissances.

Pour ce qui est de la méthodologie, la considération de variables climatiques dans les analyses d'occupation de site ainsi que la hauteur d'installation des pièges méritent d'être abordées. Au niveau des analyses statistiques, cette étude montre l'effet des précipitations et de la température sur la probabilité de détection de Grand Polatouche dans un contexte de piégeage et d'utilisation de nichoirs. À ce sens, il est pertinent de recommander l'inclusion de l'effet de ces variables sur la probabilité de détection dans les analyses de données de présence de Grand Polatouche. L'absence de considération de ces variables pourrait résulter en des conclusions erronées. Aussi, l'installation des pièges à 1.5 ou 4 m n'a montré aucun effet sur le succès de capture du Grand Polatouche. Puisque les pièges bas sont plus simples à installer et utiliser, l'utilisation de ces derniers est recommandée plutôt que les pièges hauts nécessitant l'emploi d'une échelle devant être transportée en milieu forestier.

Perspectives de recherche

Certaines questions demeurent sans réponses au terme de ce projet et de nouvelles questions sont soulevées. Parmi celles-ci, des questions sur les facteurs limitant le Grand Polatouche :

- Détermination de l'importance de la nourriture à titre de facteur limitant principal du Grand Polatouche;

- Vérification de l'hypothèse des cavités à titre de facteur limitant par la manipulation expérimentale sous la forme d'une addition de nichoirs. Cette expérience permettrait

de contrôler les autres facteurs confondants potentiellement les résultats obtenus dans le cadre de ce mémoire;

- Détermination de la présence du Grand Polatouche en forêt de conifères et détermination des types de nids utilisés dans cet habitat;

- Mesure de la valeur d'isolation thermique des 3 types de nids, soit le nid externe, la cavité et le nid souterrain;

- Caractérisation du phénomène d'agrégation dans les nids par le Grand Polatouche et description des individus impliqués;

D'autres besoins d'acquisition de connaissances sont spécifiques à l'écologie de cette espèce en forêt boréale :

- Acquisition de connaissances sur les prédateurs du Grand Polatouche en forêt boréale et taux de mortalité annuel;

- Acquisition de connaissances sur les domaines vitaux et l'utilisation de l'habitat en période d'activité nocturne;

- Acquisition de connaissances sur la diète du Grand Polatouche en forêt boréale, particulièrement en période hivernale.

BIBLIOGRAPHIE POUR L'INTRODUCTION ET LA CONCLUSION GÉNÉRALES

Aitken, K.E.H., Wiebe, K.L., and Martin, K. 2002. Nest-site reuse patterns for a cavity-nesting bird community in interior British Columbia. Auk 119(2): 391-402. doi:10.1642/0004-8038(2002)119[0391:nsrpfa]2.0.co;2.

Bakker, V.J., and Hastings, K. 2002. Den trees used by northern flying squirrels (*Glaucomys sabrinus*) in southeastern Alaska. Can. J. Zool. 80(9): 1623-1633. doi:10.1139/z02-155

Bayne, E.M., and Hobson, K.A. 1998. The effects of habitat fragmentation by forestry and agriculture on the abundance of small mammals in the southern boreal mixedwood forest. Can. J. Zool. 76(1): 62-69. doi:10.1139/cjz-76-1-62

Bednarz, J.C., Ripper, D., and Radley, P.M. 2004. Emerging concepts and research directions in the study of cavity-nesting birds: Keystone ecological processes. Condor 106(1): 1-4.

Bendel, P.R., and Gates, J.E. 1987. Home range and microhabitat partitioning of the southern flying squirrel (*Glaucomys volans*). J. Mammal. 68: 243-255.

Bowman, J., Holloway, G.L., Malcolm, J.R., Middel, K.R., and Wilson, P.J. 2005. Northern range boundary dynamics of southern flying squirrels: evidence of an energetic bottleneck. Can. J.Zool. 83(11): 1486-1494.

Brady, M.J., Risch, T.S., and Dobson, F.S. 2000. Availability of nest sites does not limit population size of southern flying squirrels. Can. J. Zool. 78(7): 1144-1149. doi:10.1139/cjz-78-7-1144

Carey, A.B. 1989. Wildlife associated with old-growth forests in the Pacific Northwest. Nat. Areas J. 9: 151-162.

Carey, A.B. 1995. Sciurids in Pacific Northwest Managed and Old-Growth Forests. Ecol. Appl. 5(3): 648-661. doi:10.2307/1941974

Carey, A.B. 2002. Response of northern flying squirrels to supplementary dens. Wildl. Soc. Bull. 30(2): 547-556.

Carey, A.B., Horton, S.P., and Biswell, B.L. 1992. Northern spotted owls - influence of prey base and landscape character. Ecol. Monogr. 62(2): 223-250.

Carey, A.B., Kershner, J., Biswell, B., and de Toledo, L.D. 1999. Ecological scale and forest development: Squirrels, dietary fungi, and vascular plants in managed and unmanaged forests. Wildl. Monogr. 142: 5-71.

Carey, A.B., Wilson, T.M., Maguire, C.C., and Biswell, B.L. 1997. Dens of northern flying squirrels in the Pacific Northwest. J. Wildl. Manage. 61(3): 684-699.

Côté, M., and Ferron, J. 2001. Short-term use of different residual forest structures by three sciurid species in a clear-cut boreal landscape. Can. J. For. Res. 31(10): 1805-1815. doi:10.1139/cjfr-31-10-1805

Cotton, C.L., and Parker, K.L. 2000. Winter habitat and nest trees used by northern flying squirrels in subboreal forests. J. Mammal. 81(4): 1071-1086. doi:10.1644/1545-1542(2000)081<1071:whantu>2.0.co;2.

Currah, R.S., Smreciu, E.A., Lehesvirta, T., Niemi, M., and Larsen, K.W. 2000. Fungi in the winter diets of northern flying squirrels and red squirrels in the boreal mixedwood forest of northeastern Alberta. Can. J. Bot. 78(12): 1514-1520. doi:10.1139/cjb-78-12-1514

D'Eon, R.G., Glenn, S.M., Parfitt, I., and Fortin, M.-J. 2002. Landscape connectivity as a function of scale and organism vagility in a real forested landscape. Conserv. Ecol. 6(2): 10. Available from www.consecol.org/vol6/iss2/art10 [accessed 10 June 2008].

Darveau, M., and Desrochers, A. 2001. Le bois mort et la faune vertébrée: état des connaissances au Québec. Gouvernement du Québec, Ministère des ressources naturelles,

Forsman, E.D., Otto, I.A., Sovern, S.C., Taylor, M., Hays, D.W., Allen, H., Roberts, S.L., and Seaman, D.E. 2001. Spatial and temporal variation in diets of Spotted Owls in Washington. J. Raptor Res. 35(2): 141-150.

Fryxell, J.M., Falls, J.B., Falls, E.A., Brooks, R.J., Dix, L., and Strickland, M.A. 1999. Density dependence, prey dependence, and population dynamics of martens in Ontario. Ecology 80(4): 1311-1321.

Gerrow, J.S. 1996. Home range, habitat use, nesting ecology and diet of the northern flying squirrel in southern New Brunswick. M.Sc. thesis, Acadia University, Wolfville, Nova Scotia, Canada.

Gomez, D.M., Anthony, R.G., and Hayes, J.P. 2005. Influence of thinning of Douglas-fir forests on population parameters and diet of northern flying squirrels. J. Wildl. Manage. 69(4): 1670-1682.

Hackett, H.M., and Pagels, J.F. 2003. Nest site characteristics of the endangered northern flying squirrel (*Glaucomys sabrinus coloratus*) in southwest Virginia. Am. Midl. Nat. 150(2): 321-331.

Hamer, T.E., Hays, D.L., Senger, C.M., and Forsman, E.D. 2001. Diets of Northern Barred Owls and Northern Spotted Owls in an area of sympatry. J. Raptor Res. 35(3): 221-227.

Heinrichs, J. 1983. The winged snail darter. J. Forest. 81: 212-215, 262.

Hokkanen, H., Törmälä, T., and Vuorinen, H. 1982. Decline of the flying squirrel *Pteromys volans* L. populations in Finland. Biol. Conserv. 23: 273-284.

Holloway, G.L. 2006. Flying squirrel (*Glaucomys sabrinus* and *G. volans*) habitat use and ecology in landscapes managed with partial harvesting silviculture in central Ontario. Ph.D. dissertation, University of Toronto, Toronto, Ontario, Canada.

Holloway, G.L., and Malcolm, J.R. 2006. Sciurid habitat relationships in forests managed under selection and shelterwood silviculture in Ontario. J. Wildl. Manage. 70(6): 1735-1745.

Holloway, G.L., and Malcolm, J.R. 2007. Nest-tree use by northern and southern flying squirrels in central Ontario. J. Mammal. 88(1): 226-233. doi:10.1644/05-MAMM-A-368R2.1.

Hurme, E., Mönkkönen, M., Nikula, A., Nivala, V., Reunanen, P., Heikkinen, T., and Ukkola, M. 2005. Building and evaluating predictive occupancy models for the Siberian flying squirrel using forest planning data. For. Ecol. Manag. 216(1-3): 241-256.

Hurme, E., Mönkkönen, M., Sippola, A.L., Ylinen, H., and Pentinsaari, M. 2008. Role of the Siberian flying squirrel as an umbrella species for biodiversity in northern boreal forests. Ecol. Indic. 8(3): 246-255.

Hurme, E., Reunanen, P., Mönkkönen, M., Nikula, A., Nivala, V., and Oksanen, J. 2007. Local habitat patch pattern of the Siberian flying squirrel in a managed boreal forest landscape. Ecography 30(2): 277-287.

Lehmkuhl, J.F., Kistler, K.D., Begley, J.S., and Boulanger, J. 2006. Demography of northern flying squirrels informs ecosystem management of western interior forests. Ecol. Appl. 16(2): 584-600.

Lomolino, M.V., and Perault, D.R. 2001. Island biogeography and landscape ecology of mammals inhabiting fragmented, temperate rain forests. Glob. Ecol. Biogeogr. 10(2): 113-132.

Martin, K., and Eadie, J.M. 1999. Nest webs: A community-wide approach to the management and conservation of cavity-nesting forest birds. For. Ecol. Manag. 115(2-3): 243-257. doi:10.1016/s0378-1127(98)00403-4

Maser, C., Anderson, R., and Bull, E.L. 1981. Aggregation and sex segregation in northern flying squirrels in northeastern Oregon, an observation. Murrelet 62: 54-55.

McDonald, L. 1995. Relationships between northern flying squirrels and stand age and structure in aspen mixedwood forests in Alberta. *In* Relationships between stand age, stand structure, and biodiversity in aspen mixedwood forests in Alberta. *Edited by* J.B. Stelfox. Jointly published by Alberta Environmental Centre (AECV95-R1), Vegreville, AB, and Canadian Forest Service (Project No. 0001A), Edmonton, AB. pp. 227-240.

McLaren, M.A., Thompson, I.D., and Baker, J.A. 1998. Selection of vertebrate wildlife indicators for monitoring sustainable forest management in Ontario. Forest Chron. 74(2): 241-248.

Menzel, J.M., Ford, W.M., Edwards, J.W., and Menzel, M.A. 2004. Nest tree use by the endangered Virginia northern flying squirrel in the central Appalachian mountains. Am. Midl. Nat. 151(2): 355-368.

Menzel, J.M., Ford, W.M., Edwards, J.W., and Terry, T.M. 2006. Home range and habitat use of the Vulnerable Virginia northern flying squirrel *Glaucomys sabrinus fuscus* in the Central Appalachian Mountains, USA. Oryx 40(2): 204-210. doi:10.1017/S0030605306000494

Meyer, M.D., North, M.P., and Kelt, D.A. 2005a. Fungi in the diets of northern flying squirrels and lodgepole chipmunks in the Sierra Nevada. Can. J. Zool. 83: 1581-1589.

Meyer, M.D., Kelt, D.A., and North, M.P. 2005b. Nest trees of northern flying squirrels in the Sierra Nevada. J. Mammal. 86(2): 275-280.

Meyer, M.D., North, M.P., and Kelt, D.A. 2007. Nest trees of northern flying squirrels in Yosemite National Park, California. Southwest. Nat. 52(1): 157-161.

Mönkkönen, L., Reunanen, P., Nikula, A., Inkeroinen, J., and Forsman, J. 1997. Landscape characteristics associated with the occurrence of the flying squirrel Pteromys volans in old-growth forests of northern Finland. Ecography 20(6): 634-642.

Mowrey, R.A., and Zasada, J.C. 1984. Den tree use and movements of northern flying squirrels in interior Alaska and implications for forest management. *In* Fish and wildlife relationships in old-growth forests: proceedings of a symposium, Juneau, Alaska, 12-15 April, 1982. *Edited by* W.R. Mechan, T.R.Jr. Merrell, and T.A. Hanley. American Institute of Fishery Research Biologists, Juneau, Alaska. pp. 351-356.

Muul, I. 1968. Behavioral and physiological influences on the distribution of the flying squirrel, *Glaucomys volans*. Misc. Publ., Mus. Zool., Univ. Mich. 134: 1-66.

Payne, J.L., Young, D.R., and Pagels, J.F. 1989. Plant community characteristics associated with the endangered northern flying squirrel, Glaucomys sabrinus, in the southern appalachians. Am. Midl. Nat. 121(2): 285-292.

Pyare, S., Smith, W.P., Nicholls, J.V., and Cook, J.A. 2002. Diets of Northern Flying Squirrels, *Glaucomys sabrinus*, in Southeast Alaska. Can. Field-Nat. 116(1): 98-103.

Ransome, D.B., and Sullivan, T.P. 1997. Food limitation and habitat preference of *Glaucomys sabrinus* and *Tamiasciurus hudsonicus*. J. Mammal. 78(2): 538-549.

Ransome, D.B., and Sullivan, T.P. 2003. Population dynamics of *Glaucomys sabrinus* and *Tamiasciurus douglasii* in old-growth and second-growth stands of coastal coniferous forest. Can. J. For. Res. 33(4): 587-596. doi:10.1139/x02-193

Ransome, D.B., and Sullivan, T.P. 2004. Effects of food and den-site supplementation on populations of *Glaucomys sabrinus* and *Tamiasciurus douglasii*. J. Mammal. 85(2): 206-215. doi:10.1644/bos-118.

Reunanen, P., Mönkkönen, M., and Nikula, A. 2000. Managing boreal forest landscapes for flying squirrels. Conserv. Biol. 14(1): 218-226.

Reunanen, P., Mönkkönen, M., and Nikula, A. 2002. Habitat requirements of the Siberian flying squirrel in northern Finland: comparing field survey and remote sensing data. Ann. Zool. Fenn. 39(1): 7-20.

Rosenberg, D.K., and Anthony, R.G. 1992. Characterisitics of northern flying squirrel populations in yound second-growth and old-growth forests in western Oregon. Can. J. Zool. 70(1): 161-166. doi:10.1139/z92-023

Smith, W.P. 2007. Ecology of *Glaucomys Sabrinus*: Habitat, demography, and community relations. J. Mammal. 88(4): 862-881. doi:10.1644/06-mamm-s-371r1.1.

Smith, W.P., Gende, S.M., and Nichols, J.V. 2004. Ecological correlates of flying squirrel microhabitat use and density in temperate rainforests of southeastern Alaska. J. Mammal. 85(4): 663-674.

Waters, J.R., and Zabel, C.J. 1995. Northern flying squirrel densities in fir forests of northeastern California. J. Wildl. Manage. 59(4): 858-866.

Weigl, P.D. 1978. Resource Overlap, Interspecific Interactions and the Distribution of the Flying Squirrels, Glaucomys volans and G. sabrinus. Am. Midl. Nat. 100(1): 83-96.

Weigl, P.D. 2007. The northern flying squirrel (Glaucomys Sabrinus): A conservation challenge. J. Mammal. 88(4): 897-907.

Wells-Gosling, N., and Heaney, R.N. 1984. *Glaucomys sabrinus*. Mamm. Species No. 229: 1-8.

Wheatley, M. 2007. Fungi in summer diets of northern flying squirrels (*Glaucomys sabrinus*) within managed forests of western Alberta, Canada. Northwest. Sci. 81(4): 265-273. doi:10.3955/0029-344x-81.4.265.

Wheatley, M., Fisher, J.T., Larsen, K., Litke, J., and Boutin, S. 2005. Using GIS to relate small mammal abundance and landscape structure at multiple spatial extents: the northern flying squirrel in Alberta, Canada. J. Appl. Ecol. 42(3): 577-586. doi:10.1111/j.1365-2664.2005.01034.x.

Wilson, J.A., Kelt, D.A., and Van Vuren, D.H. 2008. Home range and activity of northern flying squirrels (Glaucomys sabrinus) in the sierra nevada. Southwest. Nat. 53(1): 21-28.

Wilson, T.M., and Carey, A.B. 1996. Observations of weasels in second-growth Douglas-fir forests in the Puget Trough, Washington. Northwestern Nat. 77(2): 35-39.